PHYSICAL COGNITION

IN GREAT APES:

PLANNING & OBJECT COMPLIANCE

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"*An Orang climbs so slowly and cautiously... Even when closely pursued, his circumspection is amazing: he shakes the branches to see if they will bear him, and then bending an overhanging bough down by throwing his weight gradually along it, he makes a bridge from the tree he wishes to quit to the next.*"

- T.H. Huxley

From: Evidence as to man's place in nature (1863)

Abstract

It has been suggested that great ape cognitive abilities evolved in response to challenges in the physical environment related to large body size. As wild orangutans travel through the forest canopy compliant branches deform under their weight, which increases the size of gaps to be crossed and poses issues of safety and stability; yet they achieve safe and effiecient locomotion. Wild orangutans also build structurally complex nests and select branches for nest-building on the basis of their compliant properties. Both of these behaviours suggest that orangutans (1) are able to consider alternative possible actions or to plan and execute appropriate sequences of actions; and (2) possess some knowledge of object compliance (flexibility). This thesis investigated these cognitive abilities in captive great apes (orangutans and bonobos) as well as human adults and children, by presenting individuals with novel problem-solving tasks (puzzle-boxes) and novel objects (locomotor supports) and observing their behavioural responses. Attempts were made to address previous issues associated with studying physical cognition in animals, and particular attention was paid to individual differences and the role of exploration when interpreting results. Studying cognitive abilities related to wild orangutan behaviour may have implications for the evolution of cognition in great apes.

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List of publications

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Declaration of author's contribution

Chapter 1: Entirely my own work

Chapter 2: ECT designed the experiment, with input from JC and SKST. ECT collected the data, analysed the data and wrote the manuscript. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 3: ECT designed the experiment, with input from JC and SKST. ECT collected the data, analysed the data and wrote the manuscript. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 4: ECT designed the experiment, with input from JC and SKST. ECT collected the data, with the assistance of Zoe Demery. ECT analysed the data and wrote the manuscript. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 5: The experiment was run by Emma-Louise Bryant as part of her undergraduate research project, under the supervision of ECT. The study was designed by ECT and EB with input from JC and SKST. ECT collected the data (from video footage), analysed the data and wrote the manuscript.

Chapter 6: ECT designed the experiment, with input from JC and SKST. ECT collected the data, analysed the data and wrote the manuscript. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 7: The study formed part of a wider project run by SKST and Sam Coward. ECT collected the data, analysed the data and wrote the manuscript. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 8: Entirely my own work

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Chapter 1

GENERAL INTRODUCTION

1.1 Animal cognition and cognitive adaptations

In the broadest sense, cognition refers to the way in which organisms perceive, process and remember information from the world around them, and how this subsequently influences their decision making (Shettleworth 2010). Cognitive mechanisms are generally thought to involve the *mental representation* of non-perceived situations, which enables *flexible* behaviour and decision making in the face of novel challenges (Tomasello and Call 1997; Seed and Tomasello 2010; Tomasello and Call 2011). Representation permits individuals to model hypothetical situations, thus permitting the 'testing' of behaviours before implementing actions (Suddendorf and Whiten 2001), or engagement in 'mental trial-and-error' (Piaget 1954). Flexibility enables an individual to have some control over its behaviour having assessed the current situation (Tomasello and Call 1997), in contrast with inflexible, hard-wired behaviours, which are innate and triggered by external stimuli, though they may appear quite complex (e.g. Fabre 1919). A key challenge in the study of animal cognition is that the exact same overt behaviour may result from entirely different underlying mechanisms (Tomasello and Call 2008; Chittka and Jensen 2011; Chittka et al. 2012).

Cognitive abilities, like morphological features, are likely shaped by natural selection in response to specific challenges, and are one way in which individuals may solve adaptive problems (Healy et al. 2009). For example, it is known that there is a relationship (albeit correlational rather than causal) between food hoarding and spatial cognition in several bird species, with hoarders having an enlarged hippocampus compared with non-hoarding species of comparable body and brain size (Sherry et al. 1992). Cognitive skills may arise in any species under particular conditions, such as habitat instability and food unpredictability (Potts 2004; Seed and Tomasello 2010), where flexible, cognitively-guided behaviour is more appropriate than innate behaviour (Seed et al. 2009a). In order to understand something about the evolution of cognition, there is a need for direct comparisons of problem-solving behaviour between species, to look for similarities and differences in performance (MacLean

et al. 2012). This enables us to ask questions about when in an evolutionary lineage a particular capacity might have arisen; what possible socio-ecological selection pressures may have driven its evolution; what the ancestral state might have been; and the extent to which phylogeny predicts variation in cognitive ability (Byrne 2000; MacLean et al. 2012).

1.2 Evolution of primate cognition

Brain size has tended to increase in absolute and relative terms throughout the primate lineage (Montgomery et al. 2010), as has cognitive ability (Fig. 1.1).

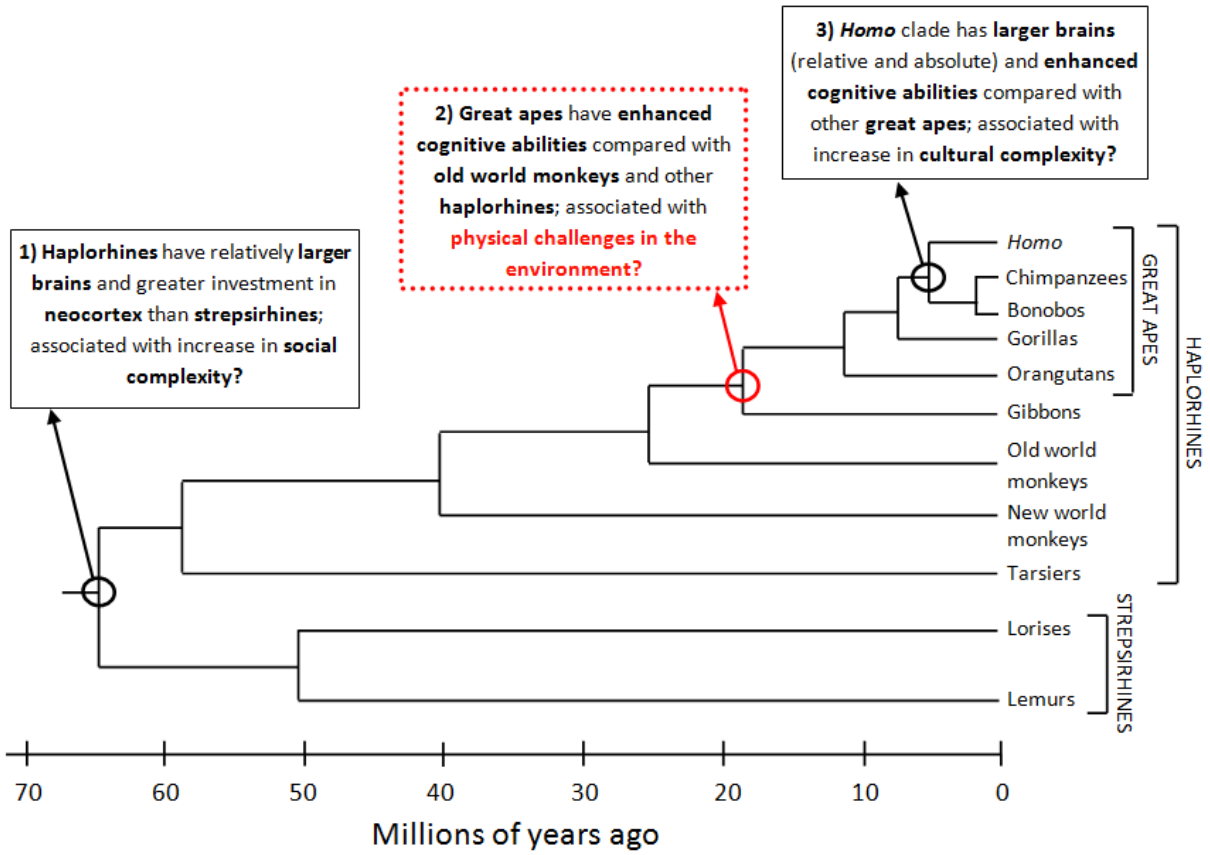

Figure 1.1 – Partial primate phylogeny highlighting key branch points/evolutionary events in primate cognitive evolution and some of the proposed selection pressures that may have driven them. Based on information from Byrne (1997)

Although brain size is easier to measure than cognition, using it as a proxy for cognitive ability is highly controversial (Healy and Rowe 2007), and there is ongoing debate regarding

which, if any, measures of brain size actually predict cognitive capacity (e.g. Deaner et al. 2007; Barton 2012). Furthermore, organisms with much smaller brains than most primates such as corvids and even some insects exhibit a diverse range of flexible behaviours (Emery and Clayton 2004; Chittka and Niven 2009; Seed et al. 2009a), so larger brains may facilitate, but do not automatically result in enhanced cognition (Chittka and Niven 2009).

Primate cognition is suggested to have evolved in response to complexities in the environment (Byrne 2000). These proposed complexities tend to be broadly grouped into one of two categories: those relating to the social world and those relating to the physical world (though these categories are somewhat overlapping and not mutually exclusive; it is highly likely that both played an important role at different points in primate evolutionary history; Fig. 1.1). Social complexities relate to other members of a community (mainly conspecifics), and were first recognised as potentially playing an important role in the evolution of primate cognition by Jolly (1966) and Humphrey (1976). Specific social challenges faced by primates have been suggested to include: life in large groups (Dunbar 1998; Maclean et al. 2008; Sandel et al. 2011); the demands of fission-fusion societies (Amici et al. 2008; Aureli et al. 2008); having to manage multiple cooperative and competitive relationships (Machiavellian intelligence; Byrne and Whiten 1988); and exchanging knowledge in cultural groups (Herrmann et al. 2007; Moll and Tomasello 2007). Physical challenges posited to have played a role in the evolution of cognitive abilities in primates include: having to locate dispersed food items (Milton 1981); extraction of concealed food items (Parker and Gibson 1977); a dependence on ripe fruit (Potts 2004); arboreal locomotion (Povinelli and Cant 1995); hierarchical processing of food items (Byrne 1995a); and nest building (Fruth and Hohmann 1996).

1.3 Great ape cognition: driven by unique physical challenges?

Challenges in the physical domain might be particularly important for understanding the evolution of great ape cognition (Fig. 1.1), given that great ape societies are no more complex than those of monkeys and so it is unlikely that social complexity alone was responsible for driving great ape cognitive evolution (Byrne 1997). Although a distinctive great ape cognition can't be confirmed by the fossil record (Begun 2004), most research to date points to the conclusion that the cognitive abilities of great apes exceed those of other non-human primates (Byrne 1997; Thompson and Oden 2000; Suddendorf and Whiten 2001; Barrett 2003; Russon and Begun 2004; Deaner et al. 2006; but see Tomasello and Call 1997 for an alternative view). For example, differences have been proposed relating to mirror self-directed behaviour (Gallup 1970; Inoue-Nakamura 1997; de Waal et al. 2005; Suddendorf and Collier-Baker 2009); the ability to form analogical concepts (Thompson and Oden 2000); and an ability to reason causally and generate plans for future events (Barrett 2003). Byrne and Bates (2010) suggested that great apes exhibit *qualitative* differences in understanding (defined as taking account of underlying meaning or causal role in an appropriate way) compared with other primate taxa, in realms as diverse as communication, tool-use, ability to imitate, and knowledge of the self as an entity.

However, findings from a number of recent studies suggest that the great ape/monkey cognitive divide might not be so clear cut. Amici and colleagues (2010) found that while apes outperformed monkeys in tasks involving the tracking of object displacements, spider monkeys (*Ateles geoffroyi*) performed comparably to or even better than some great ape species in tasks relating to object support and memory for object locations, which the authors related to high levels of fission-fusion in spider monkey societies. Similarly, Schmitt et al. (2012) compared the performance of two species of Old World monkey (long-tailed macaques (*Macaca fascicularis*) and olive baboons (*Papio anubis*)) with data previously collected from great apes in the primate cognition test battery (PCTB; Herrmann et al. 2007), which consists of 16 tasks to probe physical and social cognition

skills. They concluded that performance between the apes and monkeys was largely comparable (Schmitt et al. 2012). Although these studies both used multiple tasks, the possibility remains that cognitive differences between monkeys and apes may exist in other types of task, which might be more relevant to specific ecological challenges (the PCTB is mainly based on tests originally designed for the field of developmental psychology; Schmitt et al. 2012).

Based on evidence that there are *some* areas in which apes excel cognitively compared with monkeys, this leads us to the question of what selection pressures could have uniquely influenced a great ape common ancestor, but not other primates? Great apes in the Miocene were large-bodied, arboreal (see review by Crompton et al. 2008) and committed to a frugivorous diet in wooded habitats (Potts 2004). Having a large body in such an environment exacerbated physical challenges (Byrne 1997), particularly with respect to habitat compliance (flexibility). The canopies of forests are an incredibly complex physical environment in which arboreal animals must travel, find food and mates, and avoid predators. Problems unique to this particular niche, compared to those faced by large-bodied animals that spend a relatively large proportion of time on the ground, are (1) spatial discontinuity (gaps) in the canopy, which change dynamically as a result of the compliant properties of supports and the actions of the animal, and (2) the fragility and compliance of arboreal supports in the form of branches and lianas (Povinelli and Cant 1995). The mechanical problems of arboreality are enhanced at the terminal branch niche, as branches naturally taper towards their periphery, and therefore deform more readily under an animal's weight (Grand 1972). This is where the majority of edible ripe fruits and leaves are located (Cant 1992).

Povinelli and Cant (1995) suggested that arboreal gap-crossing is the most significant problem that is unique to large-bodied, arboreal animals because, compared with smaller-bodied animals: (1) habitat strength is reduced (so there is more chance of breakage); (2) supports become less stable (and deform more readily); (3) downward deformation

of supports increases the width of gaps to be crossed; and (4) there is an increased risk of serious injury or even death. Smaller-bodied animals are still confronted with these problems, but they don't have to incorporate and respond to new information constantly, as the surrounding habitat does not change as much in response to their body mass. They are usually able to solve the problems of compliance via stereotyped behaviour patterns, or discrete action schemata, and the risk of mortality in the event of a fall is considerably lower (Povinelli and Cant 1995). For a large-bodied animal in this situation it would be a great advantage to be able to 'mentally try out', or represent, the consequences of different potential courses of action in order to form an appropriate plan before actually executing actions, because of the potentially high costs associated with trial-and-error learning (Povinelli and Cant 1995). Other aspects of physical cognition relevant to achieving safe and effective locomotion in the canopy include an understanding of the compliant properties of supports, knowledge of gravity, and the ability to judge the size of a gap in the canopy relative to oneself.

Another behaviour seen in extant great apes but not monkeys is nest-building, which Fruth and Hohmann (1996) have argued may have enabled large-bodied ape ancestors, which were strong enough to bend and break branches, to form 'feeding nests' in the terminal branch niche, to exploit food items which were inaccessible to other species. It has also been suggested that having such a large body necessitated the building of sleeping nests to increase stability and safety in the canopy during the night (Byrne 1997). Nest construction is an example of physical problem-solving that involves selection of materials with appropriate compliant properties, complex object (branch) manipulation, and the combination of supports in a particular sequence (Healy et al. 2008; Stewart et al. 2011; van Casteren et al. 2012). Raby and Clayton (2009) claim that nest-building behaviour results from the triggering of a fixed action pattern, and there is "no evidence of planning" being involved (p.315). However, little is known about the cognitive processes underlying nest-building (Healy et al. 2008), and there is no reason to expect that they should be

any less complex than those frequently assumed to be involved in tool use (Hansell and Ruxton 2008).

It seems that two key features link arboreal locomotion and nest-building for great apes: (1) the ability to consider alternative possible actions, or perform multiple actions in an appropriate sequence (i.e. planning, as defined in section 1.5); and (2) some knowledge of the compliant properties of objects.

1.4 Orangutans as a focal species

Orangutans (*Pongo* spp.) are the largest extant arboreal mammals and are highly sexually dimorphic, with males and females averaging approximately 86kg and 38kg respectively (Markham and Groves 1990). They are the only great ape species to remain exclusively in the terminal branch niche, where their diet consists largely of ripe fruits, which is believed to have been the habitat of the great ape common ancestor during the Miocene (Begun 2004; Potts 2004). We cannot expect any living great ape to resemble the last common ancestor (LCA) of all great apes (Crompton et al. 2010), and it can be assumed that orangutans have refined their arboreal adaptations in the last 14 million or so years since their divergence from the LCA. However, as the only great ape to have retained a predominantly arboreal existence, they provide a key model for interpreting and understanding the shared features of all extant great apes (Thorpe and Crompton 2006).

Observing the apparent function of cognitive abilities in extant organisms may provide valuable clues as to their phylogenetic origin (Byrne 2000). Wild orangutan behaviour is indicative of short-term planning, as well as some understanding of compliance in the context of both arboreal locomotion and nest building. For example, orangutans rarely reach arboreal 'dead ends' during their locomotion (Thorpe, personal observation) and exhibit tree-sway to cross gaps, which has been argued to involve foresight (Chevalier-Skolnikoff et al. 1982) and reduce energy expenditure (Thorpe, Crompton and Alexander

2007). Recent evidence suggests that wild adult male orangutans may also exhibit longer-term planning, by using their long call to indicate their intended direction of travel direction up to one day in advance (van Schaik et al. 2013). There is also increasing evidence that orangutans may use diameter as a proxy for support compliance during both locomotion (Thorpe and Crompton 2005) and nest building (van Casteren et al. 2012, 2013). These behaviours are discussed in more depth in relevant experimental chapters.

On this basis, captive orangutans were chosen as a starting point for investigating planning ability and knowledge of object compliance in novel problem-solving contexts. Where possible, comparisons were made with other great apes, specifically bonobos (*Pan paniscus*) and humans (*Homo sapiens*), in order to increase the breadth of our knowledge of these aspects of physical problem-solving ability, and potentially understand something about their evolution. Orangutans and bonobos are of particular interest in the investigation of cognitive abilities from a comparative perspective because they represent our most distant and closest great ape relatives, respectively, and therefore potentially allow inferences regarding the evolution of particular abilities to be drawn (Mulcahy and Call 2006b).

In the following two sections I will define and describe in more detail the type of planning and knowledge of compliance that is of interest in this thesis, and review some of the experimental work that has been carried out in these two areas to date. Rather than being exhaustive I aim to highlight examples that are particularly relevant to the experiments presented in this thesis; further examples are discussed in more depth in subsequent chapters as appropriate.

1.5 Planning in the context of physical problem-solving

The type of planning of interest in this thesis, because of its ecological relevance to the great apes, can be described as short-term planning, or planning for *current needs* in a physical problem-solving context. (This is not to be confused with planning for

future needs, which is a hotly contested topic in the field of animal cognition; see e.g. Suddendorf et al. 2009; Osvath 2010). It can be defined as the ability to identify and execute an appropriate sequence of actions, or consider alternative possible courses of action prior to execution. In the context of physical problem-solving, as well as being able to form a plan, individuals who have an understanding of the 'folk physics' (Povinelli 2000) of a task will be more effective at generating an appropriate solution. This type of planning occurs during means-end reasoning and goal-directed behaviour, where primary perceptual information and the current motivational state of an individual stimulates a mental representation of the problem and the desired outcome, and ensuing behaviours are directed towards accomplishing that goal (Suddendorf and Whiten 2001; Raby and Clayton 2009). This ability to 'observe' imagined consequences through mental simulation, together with drawing inferences from previous experience and knowledge, enables the assessment of the likely outcome of different actions and the anticipation of possible difficulties that may be encountered during problem-solving in the absence of trial-and-error acquisition of behaviour (Byrne 1995b). (It should be noted that in talking about mental simulation I am not implying anything about animal consciousness or subjective experience; see e.g. Shettleworth 2001; Byrne and Bates 2006).

In humans, this type of planning is typically investigated using tower tasks (e.g. Tower of London; Shallice 1982), in which the aim is to rearrange a number of coloured discs on a set of pegs so that they match the configuration of discs on a goal set of pegs. Such a task is inappropriate for use with non-human animals, given that verbal instructions are required to explain the aim and rules. Some attempts have been made to use the exact same tasks as those used in developmental psychology to test non-human animals, such as combining seriated cups, but subjects require extensive pre-training just to ensure that they grasp the aim of the task (e.g. Johnson-Pynn et al. 1999). The most commonly employed test of short-term planning ability in non-human animals seems to be sequential tool use, or meta-tool use. In the simplest form of sequential tool use, a tool is used to access a second

tool, which is subsequently used to access a reward. The number of intermediate tools can be increased, which might be expected to increase cognitive demand (Wimpenny et al. 2009). This is differentiated from the use of 'tool-sets' observed in wild chimpanzees (*Pan troglodytes*; e.g. Brewer and McGrew 1990), because in this situation all tools are used to act upon the goal (Wimpenny et al. 2009).

One of the earliest examples of this type of experiment is possibly the most impressive. Döhl (1968) presented a chimpanzee, Julia, with a double series of locked boxes (ten in total) with transparent lids, each containing a key (tool) that opened one of the other boxes. One series of five boxes and keys led to a box containing a reward, whereas the other series led to an empty box. Julia succeeded in choosing the correct initial key from two options, and had to turn away from the locked boxes to make this choice (Döhl 1968), though it is not clear how much of an influence pre-training had on her performance. An orangutan also performed successfully in a comparable task (Lethmate 1982). Julia also succeeded in navigating a magnet through increasingly complex mazes, where only one out of two possible paths led out of the maze (Rensch and Döhl 1968), again after extensive pre-training on simpler mazes. (Several workers have since investigated planning using computerised maze navigation tasks, which is discussed in chapters 2 and 3).

Since Döhl's (1968) experiment with Julia many others have adopted sequential tool use paradigms to investigate planning. Hihara (2003) found that Japanese macaques (*Macaca fuscata*) were rapidly able to master sequential stick-tool use with a single intermediate tool, though this may have been due to extensive pre-training. Also, in early trials individuals often failed to retrieve the intermediate tool (Hihara 2003). Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) succeeded in a comparable task, but had also received training in the form of previous experiments involving stick tool use (Mulcahy et al. 2005). New Caledonian crows (*Corvus moneduloides*) solved a similar task spontaneously (Taylor et al. 2007; though they are natural stick-tool users in the wild), and more recently demonstrated the ability to use three stick tools sequentially (Wimpenny et al. 2009).

Martin-Ordas et al. (2012) replicated and extended Wimpenny et al.'s (2009) study with chimpanzees, bonobos and orangutans and found the apes to be capable of using up to five tools in sequence.

Similar studies have been conducted with rooks (*Corvus frugilevus*) and stone tools (Bird and Emery 2009). Here, the apparatus consisted of three tubes with collapsible bases: a narrow tube containing a reward (too narrow for large stones to fit in), a wide tube containing a large stone and another wide tube containing a small stone. In order to release the reward subjects had use a large stone that they were presented with at the start of a trial to release the small stone, which was small enough to be inserted into the narrow tube to release the reward. Four out of four subjects solved this task from their first trial, though they had previous experience of operating the apparatus and of having to select a small stone to retrieve a reward from a narrow tube (Bird and Emery 2009).

Kuczaj and colleagues (2009) investigated the planning skills of two bottlenose dolphins (*Tursiops truncatus*) using a setup that was essentially a scaled-up underwater version of the apparatus used by Bird and Emery (2009): dropping a weight into a tube released a fish. The dolphins were trained to operate the apparatus by observing a diver dropping single weights into it, and subsequently presented with two planning tasks. In the 'multiple weight test', four weights needed to be dropped in to the tube to release a reward. Weights were initially positioned close to the tube and both dolphins continued to collect and deposit them individually. However, when the cost of doing this was increased by positioning the weights further from the tube, both dolphins rapidly adopted a strategy of collecting multiple weights at once (which they had never been trained to do), thus increasing the efficiency of their problem-solving (Kuczaj et al. 2009). In the 'retaining weight box test' there were three versions of the apparatus, each requiring a single weight to release a reward inside. Two of the tubes had open bases so that the weight fell out of the bottom and could be re-used, whereas the retaining tube (which was clearly marked) had a closed base and hence trapped the weight. When the experimental setup was adjusted so that

the dolphins could look at all of the tubes once they had picked up the weight, both subjects adopted a strategy of visiting the retaining apparatus last in the majority of trials (though no statistics are presented so the significance of these results are unknown), thus maximising the number of rewards obtained (Kuczaj et al. 2009). Taken together, these results show both dolphins spontaneously succeeded in (a) increasing the efficiency of their problem-solving, and (b) maximising their reward by performing actions in a particular sequence in a novel context. It would be interesting to see how they would perform if the complexity of this task was increased, by increasing the number of apparatuses and modifying them so that they had to be used in an obligatory sequence (e.g. in a task akin to Döhl's (1968) series of locked boxes).

This focus on investigating planning using sequential tool use tasks may stem from the field's fascination with tool use in general, which perhaps derives from the old idea of 'man the tool-maker' (Seed and Byrne 2010), and the associated assumption that tool use is indicative of advanced cognitive abilities (Hansell and Ruxton 2008). However, presenting tool use tasks when what we are really interested in is planning immediately biases against non-tool users, which is a particular issue for comparative work (see section 1.7 for additional discussion of similar issues). Although many non-tool users are capable of using tools in captivity, and in some cases have demonstrated comparable or superior knowledge of physical causality to closely related tool-users (e.g. woodpecker finches (*Cactospiza pallida*) and small tree finches (*Camarhynchus parvulus*); Teschke et al. 2011), tool use is known to pose its own cognitive demands (e.g. in addition to the planning demands of a task), even for chimpanzees that are natural tool users (Seed et al. 2009b). Another issue is that the majority of sequential tool use studies have involved at least some pre-training of task components. Although it only seems fair to train animals in the basic components of a task so that the focus is then on the planning aspect, this increases the possibility that individuals could succeed through chaining previously learnt task components together (e.g. Epstein et al. 1984). An alternative approach might be

to present tasks where the motoric aspects are so simple that they require little to no training to acquire, thus reducing the issue of chaining. This would also render tasks more appropriate for comparative work with diverse species.

Planning during physical problem-solving has also been investigated by presenting animals with puzzle-boxes that require a specific sequence of actions to be performed to open them and retrieve a reward, and examining the effect of allowing a preview period on performance. Dunbar et al. (2005) presented chimpanzees, orangutans and children with puzzle-boxes that differed in the number of actions required to open them, and gave half of the subjects the opportunity to examine the boxes (and potentially plan their response) before being allowed to try and open them. Only children showed an effect of having had a preview period (Dunbar et al. 2005). However, some features of this study are problematic. The nature of the preview period differed between children and apes; children were asked to draw the boxes, whereas boxes were simply left outside the enclosures of the apes. It is possible that the apes did not attend to them at all. The performance measure was the time taken to open the boxes, which may not be appropriate given that there was no instruction to open the boxes as quickly as possible (this is obviously not possible with non-human apes), and engaging in problem-solving may be rewarding in its own right (Miyata et al. 2011; Clark and Smith 2013). Keas (*Nestor notabilis*) were presented with a similar type of task in which they had to undo multiple locks, some of which required sequential manipulations, to gain access to rewards (Miyata et al. 2011). A preview period of 10-30 seconds did not improve their performance in terms of initial accuracy, but they did correct errors more readily compared with birds that had not had an opportunity to preview the apparatus (Miyata et al. 2011).

The preview paradigm is an interesting one, but in the absence of being able to instruct subjects to plan their response (which has been shown to improve planning performance in humans, e.g. Phillips et al. 2001) it is difficult to know if subjects are actually attending to relevant task features or considering their response during that time. Furthermore there

is arguably no real incentive to open the boxes correctly the first time as errors are easily correctible, so there may be little motivation to plan a response before starting.

1.6 Compliance in the context of physical problem-solving

Compliance is an 'invisible' object property: unlike length, shape and diameter it cannot be perceived using vision alone (though in natural materials diameter may be approximately correlated with compliance). Weight is another example of an invisible object property. Perceptually salient features have received much attention in the study of physical cognition (e.g. Chappell and Kacelnik 2002, 2004; Mulcahy et al. 2005; Bird and Emery 2009); much less is known about properties that are not directly perceivable using vision. It seems surprising that there has not been more research into great apes' understanding of object compliant properties, given its ecological relevance and possibly important role in their cognitive evolution (see section 1.3). Again, the vast majority of studies have examined knowledge of compliance in the context of tool-use, and therefore many of the limitations that were described for using sequential tool use to investigate planning (see section 1.5) also apply here.

Povinelli and colleagues (2000) investigated the ability of seven captive chimpanzees to select between two rakes; one with a compliant rubber head (non-functional tool) and the other with a rigid wooden head (functional tool); when attempting to retrieve an out-of-reach reward (the 'flimsy-tool' problem). Only the tool with the rigid head had appropriate compliant properties for raking in the reward. The study subjects were allowed to obtain experience with the different tools in the context of free play, and the experimenter further demonstrated the relevant tool properties to them prior to testing. In each trial, the two rakes were prepositioned with a reward in front of each head and the subject could choose to pull one of the two rakes towards them. All subjects apart from one responded exactly as would be expected by chance (functional tool chosen in 50% of trials), suggesting that they lacked an understanding of the critical functional

properties of the tool (i.e. the compliance of the rake head) (Povinelli et al. 2000). The validity of Povinelli's (2000) findings have been criticised, because the chimpanzees were immature at the time of testing (Anderson 2001) and were reared as a peer-group, having been separated from their mothers in infancy (Whiten 2001). Evidence for the potential relevance of these factors comes from a study by Furlong and colleagues (2008), who found that nine enculturated (raised in a socio-communicatively rich environment) chimpanzees succeeded in the flimsy-tool task (see section 1.7.3 for additional discussion of how rearing history may influence cognition).

Several other researchers have conducted versions of the flimsy-tool problem with other species. Santos and colleagues (2006) presented cotton-top tamarins (*Saguinus oedipus*) and vervet monkeys (*Cercopithecus aethiops*) with pairs of cane tools, one of which was rigid (hardened clay) and the other compliant (thick rope). Subjects reliably selected the functional tool over the non-functional tool across 24 trials, implying that they recognized that a tool must be sufficiently rigid in order to rake in a reward (Santos et al. 2006). Kacelnik et al. (2006) replicated Povinelli et al.'s (2000) experiment with a captive New Caledonian crow. Interestingly, the subject chose functional tool with a rigid head in 100% of initial trials, but her performance rapidly declined over the course of each testing session, possibly due to a lack of motivation (Kacelnik et al. 2006; see section 1.7 for more discussion of non-cognitive factors that may influence task performance).

A study by Walkup and colleagues (2010) found that three orangutans given novel pairs of tools consisting of one rigid (functional) and one compliant (non-functional) tool selected the rigid tool to lever open a box containing a reward significantly more often than expected by chance. Two of the subjects did this from the first trial and the authors postulated that this either implied a pre-existing preference for rigid tools, or some level of causal understanding of relevant tool properties (Walkup et al. 2010). In a series of experiments similar to this, Manrique and colleagues (2010) investigated the ability of all four species of non-human great ape to select an appropriate tool out of sets of three tools that varied

in terms of their compliance, as well as irrelevant perceptual features such as colour. Here, subjects were either allowed to manipulate the tools, observe them being manipulated by the experimenter, or to simply look at them. This experience of the tools occurred in a separate enclosure to where the tasks were located. When subjects experienced the compliant properties of the tools, either by manipulating them directly or observing them being manipulated by the experimenter, they successfully selected, transported and used the functional rigid tool out of the sets to retrieve a food reward in two different tasks, and most did so from the initial trial. However, when they were only allowed to visually inspect the tools there was a marked reduction in performance (Manrique et al. 2010). Importantly, subjects also selected the compliant tool from sets of one compliant and two rigid tools when the task demands changed such that a compliant tool was required to retrieve the reward (Manrique et al. 2010). This suggests that they did not simply have a pre-existing preference for rigid tools as could have been the case in the study by Walkup et al. (2010). Taken together, the results of Manrique et al.'s (2010) study suggest that great apes can select appropriate tools for a task, based on their functional properties as opposed to irrelevant perceptual features such as colour. Subsequently, capuchins (*Cebus apella*) performed as well as, if not better than great apes (they were better at selecting the compliant tool) when presented with the same series of tasks (Manrique et al. 2011).

Comparable studies of the ability to extract and utilize relevant information regarding an object's compliant properties in order to meet task demands have also been conducted with human children. Klatzky et al. (2005) explored preschool children's ability to judge whether five sticks, which varied only in terms of their compliance, were appropriate for stirring either sugar or gravel. Subjects were also presented with pairs of the sticks, and asked which of the two was harder. In both tasks the children used appropriate exploratory procedures (Lederman and Klatzky 1987), such as pressing and bending the sticks, enabling them to discover their affordances without directly performing the task (Klatzky et al. 2005). Berger and colleagues (2005) investigated whether 16-month-old

toddlers considered the material properties of a handrail when attempting to cross a bridge between platforms. The handrail was either sturdy enough to support the weight of the subject (wooden), or gave way when leaned on (latex or foam). All handrails appeared rigid and stretched between the platforms without sagging. The authors found that subjects were more likely to cross narrow bridges when the handrail was sturdy as opposed to wobbly, with deformability of the handrail being determined via exploratory manipulation (Berger et al. 2005).

Taken together, evidence from studies with children (Berger et al. 2005; Klatzky et al. 2005), apes (Manrique et al. 2010) and monkeys (Manrique et al. 2011) suggests that exploratory behaviour may play an important role in understanding and learning about compliance, which is an unobservable feature of objects.

1.7 Studying physical cognition: considerations and challenges for researchers

Just as physical cognition tasks aim to pose a challenge for the animals being tested, developing appropriate paradigms is a real challenge for researchers. The aim is to design a task that isolates the cognitive capacity of interest whilst retaining some ecological validity, and present it in such a way that solving it requires subjects to use their cognitive skills flexibly (Tomasello and Call 2011). Researchers must then attempt to infer something about underlying mechanisms from the overt behaviour of non-verbal animals and try to distinguish between explanations based on, say, abstract representation of physical properties versus perceptually-based arbitrary information (Seed and Byrne 2010).

1.7.1 Captive vs. wild studies

The extent to which findings regarding the cognitive skills of captive animals can be generalised to the species as a whole (i.e. their wild counterparts) is often questioned (Tomasello and Call 2011). In the wild animals can be observed in their natural habitat

performing natural behaviours, in the environment that their cognitive abilities evolved to cope with. However, there are many potential confounding factors that cannot be controlled in the wild and the previous experience of subjects is usually unknown (not to mention the logistical challenges and expense of field research). Conducting cognitive research in captivity on the other hand permits replication and control of some of the confounding variables that are problematic in the wild, and researchers tend to have a better idea of the previous experience of their test subjects.

It has however been argued that captive populations may develop unique cognitive skills. Depending on the nature of the captive environment, cognitive skills might be expected to be limited due to a lack of physical demands (Boesch 2007); or enhanced due to the safety of the captive environment (Thornton and Lukas 2012), where food is regularly provided and there are no predators. When individuals are faced with problems that they would not come across in the wild they may also reveal skills not observed in their wild counterparts (Tomasello and Call 2008). For example, species that are not known to use tools in the wild have demonstrated proficiency comparable with tool-using species in captivity (e.g. gorillas: (Mulcahy et al. 2005) and rooks: (Bird and Emery 2009)).

Given this situation, a good approach seems to be to observe animals in the wild to find out what they do, and use this to inform controlled experimentation in captivity, with the aim of discovering something about the underlying mechanisms involved (Tomasello and Call 2008). This thesis has adopted this approach and is a step towards controlled investigation of cognitive abilities that might be related to the physical challenges faced by large-bodied arboreal animals, based on wild observations of orangutan locomotion and nest-building.

Although it is not possible to say for sure whether findings with captive animals can be generalised to the species as a whole, as Tomasello and Call (2008, p. 450) neatly put it: "if we discarded all... data from captive apes we would currently know next to nothing

about the cognitive skills of great apes".

1.7.2 Designing appropriate tasks

Having decided that the best way to address a particular research question is through controlled experiments with captive individuals, researchers next have to go about designing tasks that are appropriate for probing the cognitive ability of interest. Isolating the cognitive capacity of interest is not easy. Despite attempts to focus in on, for example, causal reasoning or planning, additional processes such as working memory or inhibitory control may simultaneously be taxed (Seed et al. 2012). Additionally, what constitutes a 'problem' and how difficult or complex it is for any given species or individual is not clearly defined (Healy 2012). There is also a need to consider the natural behavioural propensities of the species of interest to maximise the likelihood of them demonstrating how they solve a problem and thus revealing their cognitive capabilities (Shumaker and Swartz 2002). This is manageable where only a single species is of interest, but in the case of comparative cognition where the aim is to compare the abilities of potentially anatomically diverse species this is a huge challenge. Here, tasks need to be appropriate for testing species that may have very different manipulatory abilities, levels of neophobia, exploratory tendencies, visual acuity, temperament and motivation, to name but a few (Herrmann et al. 2011; Auersperg et al. 2011, 2012). All of these 'contextual' factors could influence performance, for reasons unrelated to the cognitive ability under investigation (MacLean et al. 2012; Seed et al. 2012; Thornton and Lukas 2012). It is often the case that tasks originally designed for testing a single species are subsequently used to test several other species, but with slightly modified apparatuses and methodologies, which makes comparisons problematic (Auersperg et al. 2012). The trap-tube provides a case in point. The original apparatus (Visalberghi and Limongelli 1994) was designed to test causal reasoning and required subjects to use a stick tool to retrieve a reward from a transparent tube, by avoiding a single vertical trap. Almost twenty years on, a multitude of studies with primate and bird species provides a clear example of how seemingly subtle methodological and procedural

alterations can influence performance (Table 1.1).

Table 1.1 – Summary of methodological and procedural factors that when modified have been found to improve the performance of subjects in the trap-tube and other related tasks (e.g. trap table)

Methodological/ procedural factor	Modification	Studies
Active tool use required	Tool pre-inserted in apparatus	Seed et al. (2006); Tebbich et al. (2007)
	Allow subject to manipulate reward with their fingers	Seed et al. (2009)
Tools are pre-positioned	Allow subjects to insert tool	Girndt et al. (2008)
Having to push reward away	Allow subject to retrieve reward by pulling it towards them	Mulcahy & Call (2006)

It may in fact be impossible to design a task that is equally relevant to all species, as any given task will likely be more relevant to the natural challenges faced by one species (or group of closely related species) than another (Chittka et al. 2012; MacLean et al. 2012). However, a concerted effort to design such tasks is now both timely and necessary (MacLean et al. 2012). One way of reducing the issue of comparing performance of species in a single task is to present several individuals with multiple tasks designed to probe the same or similar abilities, to reduce the likelihood of task-specific non-cognitive factors affecting performance (Herrmann et al. 2007; Herrmann and Call 2012). Another interesting approach has been to present a task that can be solved via several different methods, and blocking that method once it is discovered (Auersperg et al. 2011; Manrique et al. 2012). Such an approach reveals some of the contextual variables that influence physical problem-solving performance in different species; for example exploratory and manipulatory behaviour, as well as neophobia, were found to influence the success of keas and New Caledonian crows (Auersperg et al. 2011).

1.7.3 Dealing with the findings: small sample sizes, negative results and individual variation

Working with great apes in captivity dictates that sample sizes will likely remain small. The general approach of researchers has therefore been to suggest that, if a single individual meets the experimenter's chosen criteria for success in a given cognitive task, then the entire species has the 'capacity' to succeed (Thornton and Lukas 2012). However, whether a problem is 'solved', and therefore whether a subject is concluded to possess the capacity in question, depends entirely on the criteria set by the experimenter. Furthermore, trial success is frequently based on a binary choice (e.g. in the trap-tube) and overall task success is based on a subject succeeding in more trials than expected by chance (Thornton and Lukas 2012). There also tends to be a dichotomy in terms of explanation, in which cognition is pitched against 'just associative learning' (Seed et al. 2009a; Chappell and Hawes 2012); or 'high level' against 'low level' processes. In the case of a physical cognition task, the former might be based on flexible, transferable causal understanding (e.g. of a string being connected to a reward), whereas the latter might involve the use of arbitrary perceptual cues (e.g. continuity between string and reward). In all likelihood, most strategies will involve a combination of both or something in between the two, and such a binary approach is both over-simplistic and unnecessary.

Individual variation in performance, and particularly data from individuals that consistently fail a task, tends to be largely ignored or treated as 'noise' (Herrmann and Call 2012; Seed et al. 2012; Thornton and Lukas 2012). Negative results do not necessarily mean that a subject does not possess the cognitive ability under investigation. Rather, individuals might fail for an array of reasons, such as the 'contextual' variables described in section 1.7.2, as well as subtle methodological nuances (Table 1.1). Looking in detail at the behaviour of subjects that fail may provide a valuable insight into what strategies they might be using (Chappell and Hawes 2012; Seed et al. 2012), as well as whether their failure might be due to factors other than a lack of cognitive ability. Reducing peripheral task

demands as far as possible is one way of potentially increasing the likelihood of subjects exhibiting the cognitive ability of interest (Seed et al. 2012). In the trap-tube paradigm, for example, eliminating tool-use (and therefore the 'peripheral' cognitive load associated with it) significantly improved chimpanzees' causal reasoning ability (Seed et al. 2009b; Table 1.1).

Within captivity, rearing history may impact on an animal's cognitive abilities. Boesch (2007) has even recommended discarding all data collected from apes that have not grown up in family groups. Enculturated chimpanzees and bonobos (individuals that had spent a lot of time engaging and interacting with human caregivers in a socio-communicatively rich environment) demonstrated significantly better cognitive skills than standard-reared conspecifics, particularly in the social domain, based on a range of tasks from the PCTB (Russell et al. 2011).

None of the apes involved in the research in this thesis were enculturated, but some of them did differ in their rearing: some were mother-reared and others were hand-reared by humans. However, Russell et al. (2011) found no differences in cognitive ability between mother-reared and human-reared individuals in a group of 79 chimpanzees.

Extensive previous experience of cognitive testing may cause some individuals to become 'test savvy' (Tomasello and Call 2011), but all of the individuals in this thesis were relatively naïve to cognitive testing and had not previously been involved in any similar physical cognition research.

1.8 Aims, objectives and structure of this thesis

The overall aims of this thesis were to expand our understanding of the ability of great apes to plan during physical problem-solving, and to investigate how they might predict and explore the compliant properties of objects. An interest in these particular aspects of physical cognition stems from observed behaviour in wild apes, particularly orangutan

locomotion and nest-building. There is a need to probe the underlying mechanisms involved in these behaviours and establish whether the cognitive skills potentially involved in them can be generalised to novel problem-solving contexts under controlled conditions. In attempting to address these aims and develop paradigms for investigating them I tried to keep in mind the challenges discussed in section 1.7. In particular, I strove to develop tasks that could potentially be used to test species aside from great apes, including non-tool users. I also adopted an approach of looking at data from separate individuals in detail (including those that were unsuccessful) to try to establish what cues and strategies they might have been using when attempting to solve tasks, as well as considering the role of exploratory behaviour.

Specific questions addressed in this thesis include:

1. Are orangutans able to consider multiple obstacles related to the 'folk physics' of arboreal gap-crossing (gaps and gravity traps) when attempting to retrieve a food reward? (chapter 2)
2. Can orangutans and bonobos plan an appropriate sequence of actions (a) in a step-by-step manner; and/or (b) in advance of action in order to retrieve a food reward? How does performance in these tasks develop in children and is inhibitory control a performance-limiting factor? How do adult humans perform in the advance planning task? (chapters 3, 4 and 5)
3. Do orangutans use diameter to predict the compliant properties of barriers partially blocking passage of a food reward in a puzzle-tube? (chapter 6)
4. How do individuals explore and learn about the compliant properties of novel locomotor supports? (chapter 7)

Each empirical chapter in this thesis has been written as a stand-alone manuscript, but in some places the reader is directed back to previous sections, for example where apparatuses or methodologies were identical, in order to avoid unnecessary repetition of large sections.

In chapter 2 I describe a study in which I presented a modified version of the trap-tube apparatus to captive orangutans, to investigate whether they were able to look ahead and consider multiple obstacles (gaps, traps and barriers) when attempting to retrieve a reward item. The next three chapters (chapters 3, 4 and 5) detail experiments using a novel piece of apparatus (the paddle-box) that I designed to address some of the methodological concerns related to current tests of planning ability. In chapter 3, I adopted a comparative approach, and presented captive orangutans and bonobos with two planning tasks with different levels of complexity. In chapter 4, children were presented with the paddle-box to examine the development of their performance in the two planning tasks and establish whether the paddle-box might be an appropriate tool for investigating planning in young children, given the current lack of suitable tasks. I also attempted to examine an issue that arose in chapter 3; namely that inhibitory control could have been limiting the performance of the apes in the more complex planning task. The performance of adults in the more complex paddle-box planning task is investigated in chapter 5, because when developing new tasks to probe the cognitive abilities of animals it is important not to make assumptions regarding how human adults will perform.

Chapters 6 and 7 move away from planning to consider orangutans' understanding of the compliant properties of objects. In chapter 6 I examine whether orangutans use diameter to predict the compliance of barriers blocking their retrieval of a food reward in a puzzle-tube. A less controlled, more naturalistic approach is adopted in chapter 7 and orangutans' knowledge of compliant properties is considered in the context of their exploratory behaviour when interacting with novel compliant locomotor supports, with particular reference to their positional behaviour.

Finally in chapter 8 I attempt to summarise the key findings of this thesis and draw some overall conclusions. I also suggest some potential directions for future research.

Chapter 2

WHAT COGNITIVE STRATEGIES DO ORANGUTANS (*PONGO PYGMAEUS*) USE TO SOLVE A TRIAL-UNIQUE PUZZLE-TUBE TASK INCORPORATING MULTIPLE OBSTACLES?

This chapter, largely in its current form, is published as:

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Abstract

Apparently sophisticated behaviour during problem-solving is often the product of simple underlying mechanisms, such as associative learning or the use of procedural rules. These and other more parsimonious explanations need to be eliminated before higher-level cognitive processes such as causal reasoning or planning can be inferred. We presented three Bornean orangutans with 64 trial-unique configurations of a puzzle-tube to investigate whether they were able to consider multiple obstacles in two alternative paths, and subsequently choose the correct direction in which to move a reward in order to retrieve it. We were particularly interested in how subjects attempted to solve the task, namely which behavioural strategies they could have been using, as this is how we may begin to elucidate the cognitive mechanisms underpinning their choices. To explore this we simulated performance outcomes across the 64 trials for various procedural rules and rule combinations that subjects may have been using based on the configuration of different obstacles. Two of the three subjects solved the task, suggesting that they were able to consider at least some of the obstacles in the puzzle-tube before executing action to retrieve the reward. This is impressive compared with the past performances of great apes on similar, arguably less complex tasks. Successful subjects may have been using a heuristic rule combination based on what they deemed to be the most relevant cue (the configuration of the puzzle-tube ends), which may be a cognitively economical strategy.

2.1 Introduction

Solving naturally occurring problems in the physical environment is a key challenge faced by animals on a daily basis, and has been proposed as a selection pressure to have driven the evolution of enhanced cognitive capacities in the primate lineage (Byrne 1997). The psychological mechanisms and cognitive strategies involved in physical problem-solving are likely to vary between problems, species and even individuals (D'Mello and Franklin 2011). Some problems might successfully be solved through simple mechanisms such as associative learning and reinforcement (the mental pairing of events that occur in close temporal and spatial proximity, (Taylor et al. 2009), whereas more complex problems may require higher-level cognitive processes for efficient performance to be achieved (Kaller et al. 2011). Solving particularly complex problems might necessitate the a priori identification of an appropriate behavioural sequence, or the evaluation of alternative actions in advance of execution. Such deliberative processes (as opposed to reactive processes; Sloman 1999) might be thought of as the internal simulation of interaction with the environment, or mentally 'trying out' potential actions in short-term working memory without actually executing them (D'Mello and Franklin 2011).

Some behaviour observed in the wild is suggestive of deliberative cognitive processes. A classic example is the anecdotal observation of a single chimpanzee that used a 'tool set' consisting of different types of objects to achieve the goal of extracting honey from a bees' nest (Brewer and McGrew 1990). The processing of plant material by both mountain gorillas (*Gorilla beringei beringei*: Byrne et al. 2001) and chimpanzees (Corp and Byrne 2002) has been demonstrated to involve hierarchical, multi-stage procedures, with the authors suggesting that sequence length may be an appropriate estimate of the complexity of underlying mental processes. Another challenge posed by the physical environment, particularly for large-bodied animals, is that of arboreal locomotion. Orangutans travelling through a forest canopy face several unique challenges, particularly during gap-crossing. Successful travel requires them to make correct decisions regarding which supports to use

and avoid, as an inappropriate choice resulting in a fall, even between canopy levels, may result in serious injury or even death, particularly for larger individuals (Thorpe et al. 2009). When choosing between alternate routes they are faced with a vast amount of information to process from a multitude of potential perceptual cues, including the size of the gap to be crossed, the type and diameter of supports at either side of the gap, and how different supports are interconnected. The way that these factors interact may influence the size of a gap to be crossed. For example, effective gap sizes can change if the supports are highly compliant: these supports will bend when the orangutan applies its weight, often changing the size of the gaps between adjacent trees. Furthermore, Sumatran orangutans (*Pongo abelii*) utilize tree sway, whereby a support is oscillated to cross a gap in the canopy and progress forward (Thorpe and Crompton 2006). This often initially requires the support to be swung in the opposite direction (backwards) to the intended travel direction, in order to reach a sufficient magnitude of oscillation. Chevalier-Skolnikoff et al. (1982) suggest that such behaviour may be indicative of the internal simulation of behaviour prior to acting as opposed to physical experimentation, as during their focal period individuals always succeeded in making the transfers. Bard (1995) also found that complex physical manipulations were exhibited significantly more frequently during arboreal locomotion than in foraging by young wild orangutans in a study based on Piagetian constructs. The author interpreted these findings as a use of cognitive abilities to achieve efficient and productive travel. It was also noted that planning was only observed in a locomotor context (out of seven defined contexts during which manipulatory behaviours could potentially occur). This was in the form of two juveniles selecting appropriate routes to reach their mothers who had used tree-sway to cross a gap, which the juveniles were unable to repeat (Bard 1995). It has even been hypothesized that arboreal locomotion may have been a precipitator for self-recognition in the great apes (Povinelli and Cant 1995). It is suggested that the unique combination of problems faced by a great ape ancestor during the Miocence, specifically an arboreal lifestyle to which it became 'committed' and a large body mass, selected for the evolution

of self-conception enabling the planning and successful execution of complex locomotion through the rainforest canopy (Povinelli and Cant 1995).

The ability of animals to identify an appropriate sequence of actions or consider alternative courses of action prior to execution has been investigated experimentally in several species, but the majority of these have either involved tool use, which biases against non-tool-using species, or used computerized tasks, which requires extensive training. Suddendorf and Whiten (2001) describe experiments conducted by Döhl in the late 1960s in which a chimpanzee was able to successfully complete a multi-stage task involving unlocking a series of transparent boxes with keys, leading to a final box containing a reward. Only by assessing the obligate sequence of stages in advance was the subject able to choose the correct initial key, with the researchers claiming that she was able to successfully evaluate the task up to five steps in advance. Lethmate (1982) adapted Döhl's experimental setting for an orangutan, so that it consisted of a choice-box and four boxes with unique bolting mechanisms that could only be opened with a corresponding key. One of the boxes contained a food reward, a further two contained keys (one of which could be used to open the final box containing the reward) and the fourth was empty. The choice-box contained two keys in separate compartments that each opened one of the two key-containing boxes. Choosing one of the tools from the choice-box simultaneously blocked access to the other tool. The contents of all boxes were visible to the orangutan, enabling it to choose the correct initial key that led, via an intermediate sub-goal, to the box containing the reward. Across 400 trials the orangutan chose the correct initial key significantly more than expected by chance (in 312 trials), and the average duration of the 'phase of planning' before the initial action was 6.5 seconds (Lethmate 1982). More recently, Dunbar et al. (2005) investigated whether allowing chimpanzees, Bornean orangutans (*Pongo pygmaeus*) and children to have a prior view of a puzzle-box before attempting to open it meant that they retrieved a reward inside more quickly than when they were prevented from having a prior view, predicting that the prior view should permit them to consider the nature of the

problem and its possible solutions mentally, prior to attempting it. Although there was seemingly an improvement in performance in the prior-view condition, detailed analyses of the data revealed that this was likely a result of experience and learning due to the nature of the experimental design, rather than 'working out' their actions in advance (Dunbar et al. 2005). Further studies have investigated the ability to use tools in a means-means-end sequence (i.e. use a tool to retrieve another tool, which could be used to retrieve a food reward). Gorillas and orangutans were able to use a short tool to reach a longer tool, and only did so when the long tool was needed to reach the reward (Mulcahy et al. 2005). Japanese macaques (*Macaca fuscata*) learned how to sequentially use two tools within 50 trials after extensive training with both short and long tools (Hihara 2003). A similar study with tamarins (*Saguinus oedipus*) found that subjects were only able to succeed at a pulling task involving two tools hooked together (tools were not in spatially distinctive locations due to the species' limited manual dexterity) after sufficient training (Santos et al. 2005). In recent work on New Caledonian crows (*Corvus moneduloides*) on the other hand, some individuals succeeded at tasks requiring sequential use of 3 tools (Wimpenny et al. 2009). Some authors suggest that certain individuals may even use abstract causal rules in novel contexts (Taylor et al. 2010). Results from experiments with keas (*Nestor notabilis*) in which subjects' ability to open artificial fruit boxes requiring manipulations in multiple steps was tested suggested that in more complex tasks, permitting a preview period meant that birds were quicker to correct inappropriate actions (Miyata et al. 2011). Evidence from studies on primates and birds using computer-based tasks is also indicative of the identification of appropriate behavioural sequences prior to executing actions during problem-solving. Biro and Matsuzawa (1999) demonstrated that a chimpanzee was able to establish the correct sequence in a numerical ordering task prior to making its first choice. In 2D maze navigation tasks chimpanzees and capuchins (*Cebus apella*) solved more mazes without error than predicted by chance (Fragaszy et al. 2003). Both species were capable of self-correcting mistakes and making appropriate detours (Fragaszy et al. 2003), though a later study found that capuchins frequently made errors when the correct

path meant moving away from the global goal (Fragaszy et al. 2009). A similar study with pigeons (*Columba livia*) found evidence of planning of actions one step (and possibly two steps) in advance in computerized maze tasks (Miyata and Fujita 2008). Finally, in studies of planning behaviour with two bottlenose dolphins (*Tursiops truncatus*), subjects had to learn to reuse a weight as a tool by dropping it into boxes that resulted in a reward being released, but one of the boxes retained the weight so that it could not be reused. Both individuals rapidly learned to visit the weight-retaining box last in order to obtain a maximum reward (Kuczaj et al. 2009).

It is difficult to tease apart alternative explanations for seemingly 'intelligent' behaviour, and the underlying mechanisms are often revealed to be relatively simple (e.g. Povinelli 2000). Taylor and colleagues (2007) claimed that New Caledonian solved a sequential tool use task by using analogical reasoning, but Wimpenny et al. (2009) conducted experiments that suggested simpler processes such as chaining (the interconnection of separate behavioural repertoires, sensu Epstein et al. 1984) may be sufficient to explain successful performance. Some recent studies have specifically aimed to differentiate between behavioural strategies used during physical problem-solving. Hunt and colleagues (2006) found that wild New Caledonian crows were probably using a two-stage heuristic strategy to solve a tool-length task, whereby they initially used default behaviour, but adapted it accordingly when it failed. Heuristic rules might be employed by animals when tasks are cognitively demanding in order to reduce the effort associated with solving them (Shah and Oppenheimer 2008). Cheke and colleagues (2011) presented Eurasian jays (*Garrulus glandarius*) with a series of water-level tasks that manipulated the information that was available to facilitate learning, enabling them to infer the mechanisms by which learning occurred. The authors concluded that successful subjects seemed to rely on a combination of instrumental conditioning and causal cues (Cheke et al. 2011).

We designed a puzzle-tube task based on the trap-tube paradigm (Visalberghi and Limongelli 1994) which was designed primarily to investigate causal reasoning, but is also a useful

way of testing a subject's ability to consider the outcomes of different potential actions, with regards to the position of a trap and its impact on the path of a reward. However, unlike the original trap-tube apparatus in which the only obstacle was a single trap at one side, we incorporated multiple obstacles at both sides to investigate how orangutans might go about solving a problem involving the consideration of multiple steps and information from several perceptual cues. We also attempted to address methodological and procedural issues found to influence performance on previous trap-tube tasks, including the requirement to use tools (Seed et al. 2006; Tebbich et al. 2007), tools being prepositioned in the apparatus (Girndt et al. 2008), having to push the reward away from oneself (Mulcahy and Call 2006b) and a predisposition to avoid displacing rewards over traps (Seed et al. 2006; Tebbich et al. 2007; Martin-Ordas and Call 2009; Seed et al. 2009b). These studies showed that subjects' performances may be strongly influenced by procedural features of the experimental design. Therefore, our task uniquely combined the following features:

- It did not require tool use
- It did not require the reward to be pushed away from the subjects
- It did not always require trap avoidance for the correct response
- It was presented as trial-unique configurations, so that the configuration of obstacles had to be evaluated anew on each trial
- The number of trials was deliberately limited to minimise the possibility of the task being solved using associative learning

In the present study we investigated whether Bornean orangutans were able to consider the impact of multiple obstacles on the path of a reward, and therefore identify a priori the correct direction in which to move the reward before executing actions to obtain it. As well as establishing if subjects were able to solve the task (i.e. choose the correct direction), we examined post hoc how they might have been attempting to do so. We predicted that orangutans should perform well in such a task, given that they successfully navigate gaps in the canopy without reaching arboreal 'dead-ends', suggesting that they

decide on and follow routes prior to beginning their travel (Thorpe, personal observation). As the most distantly related of our great ape relatives, their study is also interesting from a phylogenetic perspective with regards to tracing the emergence of the cognitive capacities related to complex physical problem-solving.

2.2 Materials and methods

2.2.1 Subjects and housing

Three subjects, all mother-reared and housed at Apenheul Primate Park (Netherlands) participated in the task reported here (see Table 2.1).

Table 2.1 – Study subjects: sex, age in years and whether they were born in captivity (C) or in the wild (W)

Subject	**Sex**	**Age**	Birthplace
Amos	M	9	C
Sandy	F	27	C
Silvia	F	44	W

Eight adult orangutans (six females and two males) were initially identified for participation in the study; however five subjects were dropped following the initial phases (see 'familiarisation phase' section below for details). Both indoor and outdoor enclosures were equipped with climbing elements including tree trunks, fibreglass poles, ropes and netting, and enrichment objects such as puzzle feeders were available.

2.2.2 Apparatus: the puzzle-tube

The apparatus was attached to the outside of the enclosure and consisted of a transparent Perspex puzzle-tube (75 cm x 12 cm x 10 cm) with the following components that could be manipulated by the experimenter (see Fig. 2.1):

1. Gap-size of traps: large (4.5 cm); medium (3 cm); small (2 cm)

2. Trap direction: forwards (opening towards subject); backwards (opening towards experimenter)
3. Ends configuration: each end could be open or closed

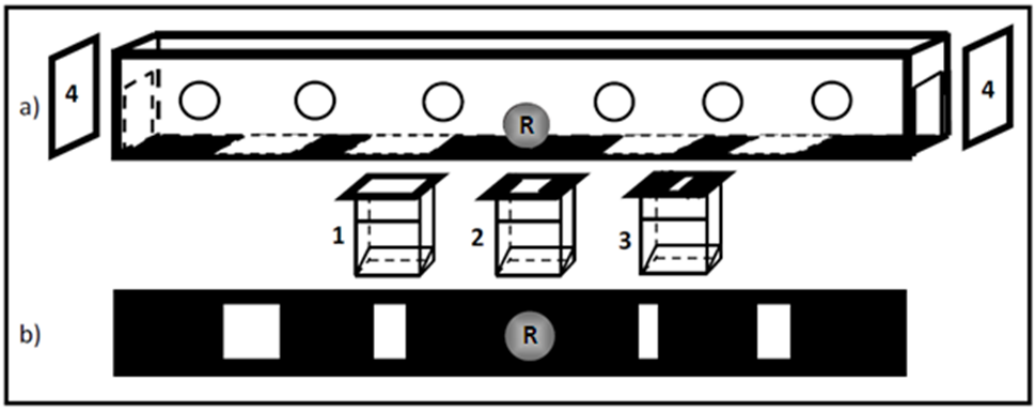

Figure 2.1 – Apparatus used in the experiment (a) showing interchangeable components: traps with large (1) medium (2) and small (3) gaps that could face either forwards (towards subject) or backwards (towards experimenter), and end pieces (4). The gap sizes were always configured in the order shown in the plan view (b), though the entire configuration could be rotated 180°. The reward (R) is shown in its central starting position for each trial

The apparatus permitted a total of four gaps in the base of the tube (two at each side of the reward's central starting position). The size of the reward (a walnut) meant that it fell through large gaps but could be displaced over small and medium gaps. If the trap beneath a large gap was facing forwards then the reward could be retrieved by the subject (for an example, see Fig. 2.2c). If on the other hand the trap was facing backwards then it was lost by the subject (as shown in Fig. 2.2d and Fig. 2.2e) and collected by the experimenter and disposed of. The direction in which the traps beneath small and medium gaps faced was irrelevant as the reward never fell into them, but they were included so that the location of a single trap type could not be used as an arbitrary cue. At one side of the puzzle-tube there was a small gap followed by a medium gap and at the other side a medium gap followed by a large gap (see Fig. 2.1b and Fig. 2.2). The basis for this configuration of gaps was that if subjects only considered the obstacles closest to the reward, i.e. the first gap that must be navigated, then we would expect them to move the reward towards the smaller of the two gaps. Thus, the initial small gap on one side of the

tube potentially acted as a perceptual 'lure', because compared to the initial medium-sized gap on the other side it should have seemed that the reward was less likely to fall through. However, as a large gap resulted in the reward being retrieved in some trials but lost in others, trap direction and the configuration of the end pieces also had to be considered. If an end of the tube was open and the two gaps on the same side were small enough for the reward to pass over, then the reward could be retrieved from the end (see Fig. 2.2a). Therefore, because there were multiple obstacles in each direction, subjects needed to look ahead and consider the effect of each obstacle on the reward in order. Only by evaluating the multiple obstacles at both sides of the puzzle-tube (the configuration of gaps, the direction in which the trap beneath the large gap was facing, and whether the ends were open or closed) before selecting the initial direction in which to move the reward could subjects achieve perfect performance. However, by attending to some cues but not others performance could still differ from what would be expected by chance (i.e. a 50% success rate; see section 2.3.4 for detailed explanation).

2.2.3 General procedure

Subjects were tested in separation rooms (10-15 m^2) where they were held on a regular basis for feeding and cleaning purposes. During the testing phase they were tested in isolation except for one adult female (Sandy) who was accompanied by two dependent juveniles. Subjects were not food deprived before the trials, water was available ad libitum and they could choose to stop participating at any time. The reward in each trial was a walnut and subjects remained motivated to obtain them throughout the study. Subjects manipulated the reward through a series of finger holes (see Fig. 2.1a) and could retrieve the reward either via an open end of the tube or a forward-facing trap beneath a large gap.

Familiarisation phase

All eight potential subjects were presented with the puzzle-tube in its simplest configuration, with a continuous solid base (no gaps or traps) and both ends open. This tested whether the ability to access the reward by rolling it out of either end of the tube was within their sensorimotor repertoire and also familiarised them with the apparatus to minimise the risk of neophobic responses during the testing phase. Four subjects were dropped from the study at this stage due to a lack of interest, motor problems or becoming too nervous or frustrated in the separation areas. Following baseline testing the remaining four subjects then participated in a simpler task (the gap-size task) than the one reported here, consisting of 32 trial-unique configurations that incorporated only a single gap at each side of the tube, which could be small or large (basic methods and data for this task are provided in Appendix A). Subsequently a further subject was dropped from the study as she repeatedly attempted to squeeze the reward through the central finger hole rather than moving it in either direction from its central starting position. The remaining subjects that participated in the testing phase were Amos, Sandy and Silvia (see Table 2.1).

Testing phase

Based on the three puzzle-tube variables (gap-size, trap direction and ends configuration) we generated 64 trial-unique configurations (32 oriented left and right), three schematic examples of which are shown in Fig. 2.2.

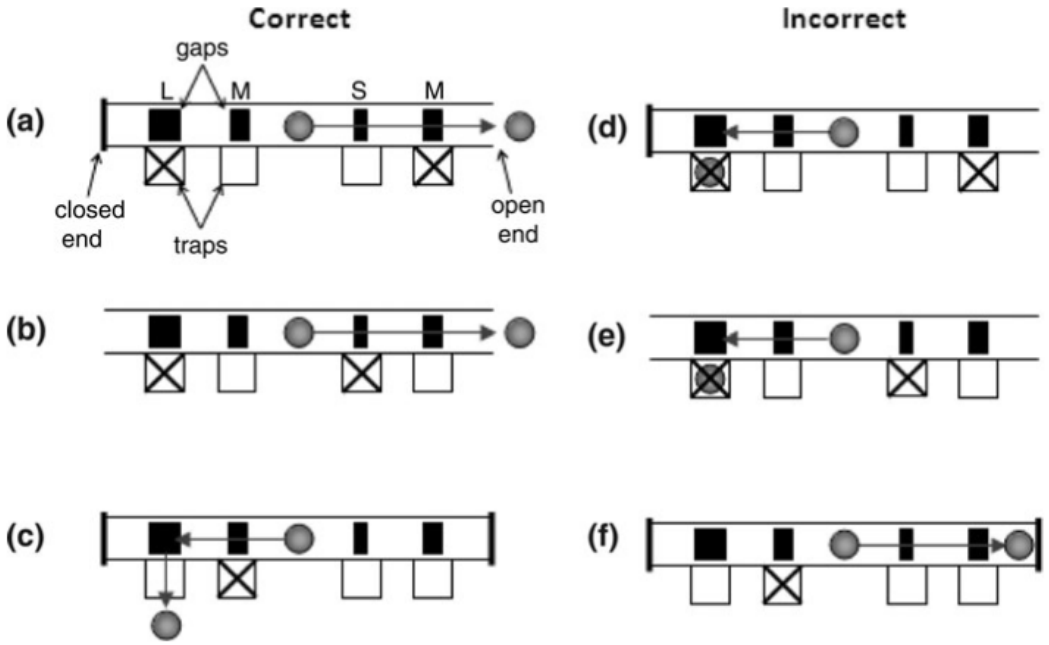

Figure 2.2 – Three schematic example configurations of the puzzle-tube apparatus showing both gap-size (L= large; M= medium; S= small) and trap-direction (open box= forwards-facing; crossed box= backwards-facing), as well as ends configuration (open or closed). Examples of the correct direction in which to move the reward (direction of arrow) and the access point for obtaining it (head of arrow) are shown (a - c); and the outcome for the same three example configurations if the incorrect direction is chosen (d – f)

Limiting the total number of trials minimised the opportunity for learning across the task and reduced the chance of the task being solved through associative learning and reinforcement. These 64 trials were pseudorandomised into 6 blocks of either 11 (blocks 1-4) or 10 (blocks 5 and 6) trials. Order of block presentation was randomised for each subject. Subjects received one block per day, with session referring to the sequential order in which the blocks were presented.

In each trial, the test subject was presented with the empty apparatus for a preview period of up to 20 seconds, though this was cut short if the subject lost interest in the apparatus or became frustrated. The reward was then placed in the centre of the puzzle-tube for the subject to manipulate. In each trial the reward could be retrieved if it was moved towards one side but not the other (the 'correct' side varied between trials). Fig. 2.2 shows some schematic examples of the outcomes of moving the reward in the 'correct' (Fig. 2.2a-c)

and 'incorrect' (Fig. 2.2d-f) directions.

2.2.4 Data scoring and analysis

All trials were videotaped. For each trial we scored whether the initial choice of direction (defined as the direction in which the subject first moved the reward, even if this was subsequently switched) was correct or incorrect, and whether it was to the left or right. Subjects were allowed to correct their mistakes if they chose the incorrect initial direction, so in some 'incorrect' trials they eventually went on to retrieve the reward. If a mistake was corrected prior to the reward reaching an impeding obstacle (closed end or large backwards-facing gap) this was scored as 'self-corrected'. The dependent measure was the percentage of correct responses defined as choosing the correct initial direction in a trial. Two-tailed binomial tests were used to assess whether individual subjects' initial choice of direction across the 64 trials differed from what would be expected by chance (50% correct) and also whether they showed any directional preferences. The alpha value for the significance level was always 0.05. Data were analysed using PASW Statistics 18 (IBM SPSS Inc. 2009) and R 2.11.1 (LME4 package, R Development Core Team 2010).

Rule simulations

When attempting to solve the task, subjects could have used the configuration of one or more of the obstacles as a cue for choosing the direction in which to move the reward. To explore whether this might have been the case we generated simulated performance outcomes (% correct responses) semi-manually using a computer for the 64 trials based on five different procedural rules and six rule combinations (see Fig. 2.4 caption for details of rules) and plotted these together with subjects' performances (Fig. 2.4). For example, if subjects chose the initial direction in which to move the reward based on the procedural rule 'always move the reward away from the large gap' ('avoid L gap' in Fig. 2.4), we could produce a simulated '% correct responses' outcome by examining each of the 64 trials in turn and generating an initial choice of direction based on following that rule, and

determining whether this would have been correct or incorrect for that particular trial. For rule combinations, rules were used in sequence on each trial until an unambiguous outcome was achieved (i.e. the reward was either gained or lost). For example, for the rule combination 'O end/L gap' (see Fig. 2.4), in all trials where there was only one open end the reward was moved towards it (first rule: 'O end'). However, in trials where both ends were configured the same the rule 'O end' generated an ambiguous outcome, so the second rule ('L gap') was used; i.e. the reward was moved towards the large gap, resulting in the reward either being gained or lost. For rules and rule combinations that involved direction being chosen at random (decided by random numbers generated in Excel), the simulation was repeated 10 times to give a range of possible outcomes (n=640).

GLMMs

We used generalised linear mixed modelling (GLMM) (Crawley; 2007; Melis et al.; 2011) to assess the effects of testing session (1-6) and the puzzle-tube variables (ends configuration, gap-size and trap direction) on whether the initial choice of direction was correct or incorrect. Only one gap-size was used in the models as the configuration of gaps was always as shown in Fig. 2.1b (or rotated through 180 degrees).

2.3 Results

2.3.1 Initial choice of direction

Amos' and Sandy's performances differed significantly from chance-level (50% correct) across the 64 trials (binomial test: 51 out of 64 trials correct; $p<0.0001$ and 43 out of 64 trials correct; $p=0.008$ respectively, see Fig. 2.4). Silvia chose the correct initial direction in 25 out of 64 trials, which was below chance level but not significantly so (binomial test: $p=0.103$). Fig. 2.3 shows subjects' performances across consecutive testing sessions.

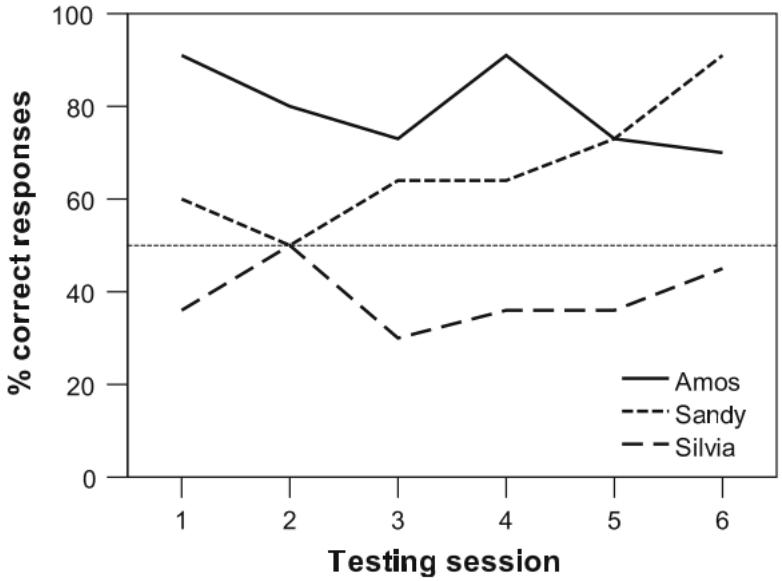

Figure 2.3 – Percentage of correct responses by each subject across the six consecutive testing sessions. There was no significant improvement in subjects' performances, though Sandy's performance did show a net improvement. Horizontal dotted line indicates chance-level performance (50% correct)

Amos' performance differed significantly from chance level in his first testing session (binomial test: 10 out of 11 trials correct; p=0.012; see Fig. 2.3). Amos and Sandy both chose the correct initial direction in the first trial in five out of the six testing sessions, including the first trial of their first sessions. Amos' performance ranged from 70-91% of trials correct within a session, and Sandy's from 50-91%. Sandy's performance showed a net overall improvement in performance across sessions (see Fig. 2.3); this was tested quantitatively in the GLMMs below. Silvia's best within-session performance was 50% of trials correct in session 2, with her poorest performance occurring in session 3 (30% of trials correct, see Fig. 2.3).

2.3.2 Directional preferences

Neither Amos nor Sandy showed a directional preference across the 64 trials (binomial test: p=0.53 and p=0.10, respectively). Silvia on the other hand showed a significant overall preference to move the reward to the right (64.1% of trials; binomial test: p=0.03).

2.3.3 Self-correction

Amos did not self-correct in any trials. Sandy self-corrected her initial choice of direction in 2 out of 21 (9.5%) and Silvia in 8 out of 39 (20.5%) incorrect trials. All self-corrections occurred when the impeding obstacle was a closed end of the puzzle-tube; never when it was a large backwards-facing gap. Subjects usually self-corrected following tactile exploration of the closed end.

2.3.4 Rule simulations

Subjects' individual performances and the simulated outcomes based on various rules and rule combinations are shown in Fig. 2.4.

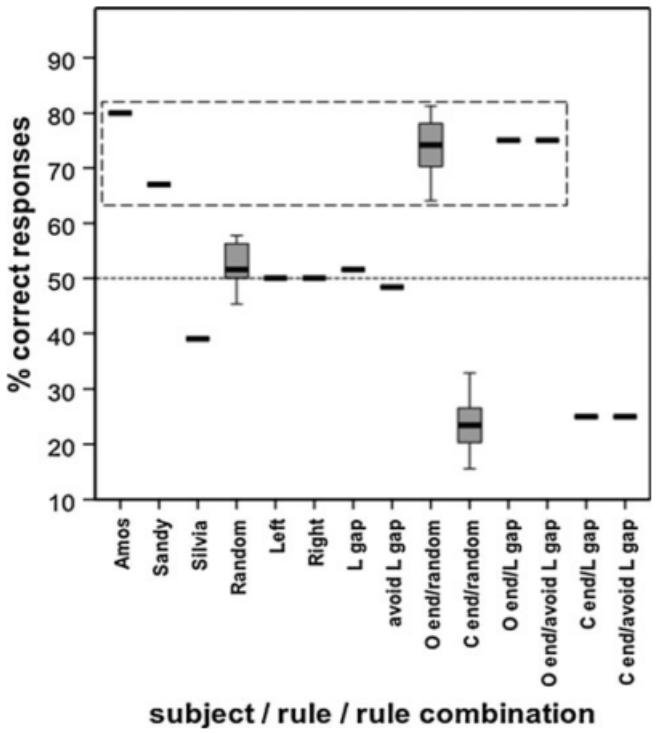

Figure 2.4 – Percentage of correct responses for the three subjects (n=64) and simulated performance outcomes based on five procedural rules and six rule combinations: Random = move reward in random direction; Left = move reward left; Right = move reward right; L gap = move reward towards large gap; avoid L gap = move reward away from large gap (n=64 for each). O end = move reward towards open end of tube; C end = move reward towards closed end of tube. For rule combinations (e.g. O end/random), rules were used in sequence on each trial until an unambiguous outcome was achieved (i.e. the reward was either gained or lost). Simulations involving direction being chosen at random were repeated 10 times to give a range of possible outcomes (n=640). For boxplots the line across the box is the median and the whiskers indicate the range of outcomes for ten repeated simulations. Dotted line indicates chance-level performance (50% correct); dashed box shows that Amos' and Sandy's performances fell within the range of simulated outcomes for the O end/random rule combination, as did the other two rule combinations involving the configuration of the open end

As Amos' and Sandy's performances both differed significantly from chance-level (see Fig. 2.4) this suggests that they were not choosing the direction in which to move the reward randomly ('Random'), or based solely on a directional bias ('Left', 'Right'). Neither were simply avoiding the large gap or succumbing to the potential 'perceptual lure' of the small gap ('avoid L gap'), nor always moving towards the large gap ('L gap'), as all of these simulations generated performance outcomes of around 50% correct (see Fig. 2.4). However, simulating directional choices for the 64 trials using the rule combination

'move reward towards open end of the tube; if not applicable choose direction at random' ('O end/random' in Fig. 2.4) generated a range of outcomes significantly different to 50% correct (64.1 - 81.3%, Fig. 2.4). Both Amos' (79.7% correct) and Sandy's (67.2% correct) performance fell within this range (see dashed box in Fig. 2.4). Two further rule combinations based on primarily moving the reward towards the open end and secondarily moving the reward either towards or away from the large gap ('O end/L gap' and 'O end/avoid L gap' in Fig. 2.4) also resulted in a simulated performance outcome of 75% correct (Fig. 2.4). Silvia's performance did not correspond to or fall within the range of any of the simulated performance outcomes (see Fig. 2.4).

2.3.5 GLMMs

We fitted a model with initial choice of direction as a binary response, subject as a random factor, session as a covariate with fixed effect, and ends configuration (same, different), gap-size 1 (large, small; which determines other gap sizes), and the direction each trap was facing (forwards, backwards) as fixed factors. This analysis confirmed that subjects were more likely to choose the correct initial direction when the ends were configured the same, i.e. both open or both closed, as opposed to one open and one closed, as ends configuration was the only factor that influenced whether the initial choice of direction was correct or incorrect (see Table 2.2).

Table 2.2 – GLMM model output showing factors that influenced the whether the choice of initial direction was correct or incorrect

Factor	Estimate	SE	z	p
Session	0.009	0.010	0.934	0.350
Puzzle-tube variables				
Ends configuration	1.054	0.341	3.089	0.002**
Gap size 1	-0.292	0.334	-0.876	0.381
Trap 1 direction	-0.129	0.332	-0.388	0.698
Trap 2 direction	0.438	0.334	1.309	0.190
Trap 3 direction	-0.590	0.340	-1.733	0.083
Trap 4 direction	-0.494	0.341	-1.449	0.147

We compared this first full model with a model that did not include ends configuration as a fixed factor. The fit of the second more parsimonious model resulted in a significant reduction of fit (likelihood ratio test comparing the two models: χ^2=9.871; p=0.002), indicating that ends configuration explains a significant amount of variance. Notably, session had no influence on whether the initial choice of direction was correct or incorrect (see Table 2.2), i.e. there was no significant variation in performance between testing sessions. Additional analyses showed no interaction effects among the factors in the model.

Ends configuration

In the subset of trials in which the puzzle-tube ends were configured one open and one closed (n=32), Amos and Sandy chose the correct initial direction in 90.6% and 87.5% of trials respectively. In the other trials where the ends of the tube were configured the same Amos' performance was the same whether the ends were either both open or both closed (68.8%; n=32; p=0.052). Sandy's performance in this subset of trials was close to chance-level (46.9%, n=32; p=0.860), though she performed better when the ends were both closed (56.3% correct; n=16) than when they were both open (31.3% correct; n=16). This consideration of different subsets of trials supports the results of the GLMM analysis; that the configuration of the ends does indeed influence performance. Silvia's performance was below chance-level in all subsets of trials.

2.4 Discussion

We devised a novel puzzle-tube task that aimed to investigate orangutans' ability to consider the impact of multiple obstacles in two alternative paths on a reward, prior to choosing a direction in which to move it. When designing the task we aimed to minimise the methodological and procedural concerns of previous studies based on the trap-tube paradigm. We also developed a novel analytical method of rule-simulation for exploring

how subjects may have been attempting to solve the task with regards to what potential procedural rules or rule combinations might have been used.

Two of the three subjects (Amos and Sandy) solved the task (that is, performed significantly above chance) across the 64 trial-unique configurations. Importantly, Amos performed significantly above chance level in his first session, and both successful subjects responded correctly in their initial trial in 5 out of 6 sessions. These results are impressive, given that in previous studies only 2 out of 5 and 2 out of 6 orangutans solved arguably simpler tasks in which they had to learn to avoid a single trap, and required a greater number of trials to do so (Mulcahy and Call 2006b; Martin-Ordas et al. 2008). Furthermore, in both of those studies the only variation between trials was the side on which the trap appeared. Therefore, subjects could have solved the tasks based on the single procedural rule 'move the reward away from the trap'. In a study by Seed et al. (2009b) using a two-trap box that did not require tool use, all eight chimpanzee subjects learnt to avoid a trap in 40-100 trials. However, only one subject was able to successfully transfer between two tasks that required opposite responses based on the configuration of an arbitrary cue; the other seven continued to use a single procedural rule ('push toward the shelf piece') that applied to the previous task (Seed et al. 2009b).

Fragaszy et al. (2009) suggested that implementing a forced delay may support the selection of behaviours other than the prepotent one, and there is some evidence to suggest that orangutans may outperform other great ape species in tasks requiring inhibitory control (Vlamings et al. 2010). Furthermore, keas were quicker to correct mistakes when opening boxes with multiple locks following a short (10-30 second) preview period (Miyata et al. 2011). It is therefore possible that the short preview period in our experiment permitted subjects to consider the multiple obstacles at each side of the puzzle-tube prior to acting, though there were no obvious behavioural differences between subjects during this time (Tecwyn, personal observation). Dunbar et al. (2005) did not identify an effect of prior view on chimpanzees' or orangutans' speed of retrieving a reward from a puzzle-box.

However, in the past orangutans have frequently been dismissed as "sluggish, slothful and uninteresting" (Russon 2010, p. 981), which suggests that latency may not have been an appropriate measure of performance due to inter-species behavioural differences. To our knowledge this is also the first time that orangutans have been tested on a trap-tube-like task that does not require tool use, so it is possible that the additional cognitive load of having to use a tool may have been masking the species' actual understanding of such tasks in previous experiments, as was found to be the case for chimpanzees (Seed et al. 2009b).

What possible strategies could an animal potentially use when attempting to solve a novel problem and how do these relate to our task? By deliberately limiting the total number of trials reduced the potential for associative learning and reinforcement across trials, and the fact that the GLMMs did not reveal a significant effect of testing session on performance (i.e. subjects did not improve significantly at the task with additional trials, see Table 2.2 and Fig. 2.3) suggests that associative learning does not explain the performance of the successful subjects. Amos in particular provides a strong case against learning across trials, as he performed significantly above chance-level in his first testing session. Although it is possible that subjects could have learned relevant associations prior to the study, to our knowledge they had not been presented with any similar apparatus. A puzzle-feeder that had been used by Sandy and Silvia in the past involved using a stick to navigate a reward through a vertical maze, causing it to drop through a series holes and out of the bottom. Amos had never used the puzzle-feeder.

A lack of evidence for learning does not, however, eliminate the possibility that subjects were using a procedural rule from the initial trial (Fedor et al. 2008). Such a rule could be based on an arbitrary or relevant cue, and could be appropriate or inappropriate. In contrast to previous similar studies, in our task every trial configuration was unique, and no single cue (e.g. a small gap) individually identified the correct directional response, making it impossible to perform perfectly by using a single procedural rule in relation to a

single cue. However, our rule simulations (Fig. 2.4) demonstrated that on our task at least it was possible to perform significantly better than chance (though not perfectly) by using one of the three following 2-rule combinations, all of which involved an initial examination of the configuration of the puzzle-tube ends: 'move reward towards open end of the tube; if not applicable (a) choose direction at random; (b) move towards the large gap; or (c) move away from the large gap'; (see dashed box in Fig. 2.4). It is feasible that Amos and Sandy were using rule combination (a) as both of their performances fell within the range of simulated outcomes for the 64 trials based on it (see Fig. 2.4). The results of the GLMM analyses quantitatively supported the notion that successful subjects were able to use ends-configuration as a relevant cue for choosing the direction in which to move the reward when one was open and one closed, as they performed better in this subset of trials compared to when both ends of the tube were configured the same (both open or both closed). Furthermore, self-corrections only occurred when the impeding obstacle was a closed end (not a large backwards-facing gap), which suggests that subjects were able to use this as a cue, even if they did not do so prior to choosing their initial direction. Self-correcting may be indicative of a 'planful' (Willatts 1989) or forward search strategy, whereby subjects only look ahead to the obstacles in the path of the reward once it has already been moved either left or right (Fragaszy et al. 2003; Pan et al. 2011).

A further possibly more cognitively demanding strategy would be to consider different potential actions and their outcomes for each trial via deliberative processes in working memory, prior to choosing which direction to move the reward in. Amos performed above chance-level, though not significantly so (68.8% correct; n=32; p=0.052) in the subset of trials where one open end could not be used as a cue for choosing direction (as both ends were configured the same), which suggests that he may also have been able to use relevant information regarding gap-size and trap-direction to some extent. This suggests that he may have been considering obstacles other than the ends of the tube. Furthermore he was equally able to both avoid the large gap and to use it to access the reward, as he performed

equally well in trials requiring either one of these outcomes (11 out of 16 correct for both; see Fig. 2.5). It therefore seems likely that Amos was either using deliberative processes to some extent, or was able to use a number of procedural rules flexibly, depending on the configuration of cues in a given trial. Alternatively, subjects could have used deliberative processes when initially faced with the task, for example in the first or first few trials, and subsequently constructed and used rules based on this limited experience. Fig. 2.5 shows that, in fact, subjects could have achieved perfect performance by using three procedural rules (R1-R3) based on the three possible configurations of the ends of the tube and considering the position of the large gap (also see Fig. 2.2 for schematic examples of these). The numbers in shaded circles indicate the number of trials in which individual subjects chose the correct initial direction in trials with that configuration (see Fig. 2.5).

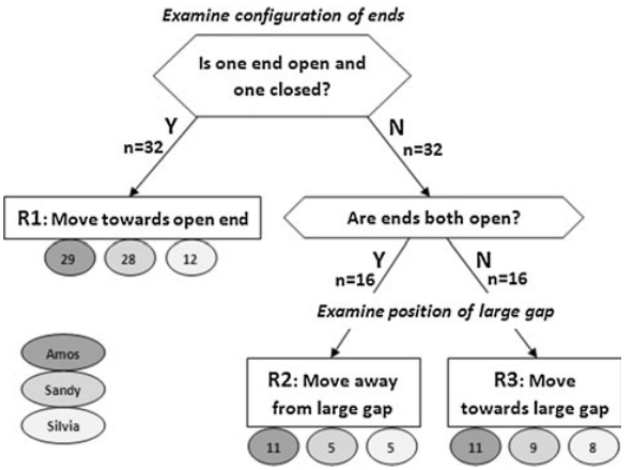

Figure 2.5 – Subjects could have chosen the correct initial direction in 100% of trials using the decision tree shown here, which is based on the configuration of the puzzle-tube ends and the location of the large gap in a given trial. When the ends of the tube were configured one open and one closed (n=32) a single procedural rule (R1) could be used to identify the correct initial direction. When the ends of the tube were configured both open (n=16) or both closed (n=16), subjects also needed to consider the position of the large gap and use a decision rule based on that (R2 or R3). Numbers in shaded circles show the number of trials in which each subject chose the correct initial direction

In Fig. 2.2, subjects could have chosen the correct initial direction in each of the three example configurations shown by using one of three rules shown in Fig. 2.5: in (a) by using rule R1; in (b) by using rule R2; and in (c) by using rule R3. Using rule R1 would

only require the subject to examine the configuration of the puzzle-tube ends, therefore these trials (n=32) could be solved by following the simple procedural rule 'move reward towards open end of the tube' (as in Fig. 2.2a). Using the other two rules (R2 and R3 in Fig. 2.5) would require both ends-configuration and the position of the large gap to be considered (as in Fig. 2.2b and 2.2c). The correct initial direction could also have been chosen in the remaining 61 configurations using the decision tree shown in Fig. 2.5. But why would subjects use procedural rules (if indeed this is what they were doing) rather than considering each trial individually, and is one approach more cognitively demanding than the other? Shah and Oppenheimer (2008) suggest that the use of heuristic rules in problem-solving, for example examining fewer cues, may reduce cognitive effort (in humans at least) by decreasing the amount of information to be held in working memory at a given time. Such rapid, simple strategies may be advantageous in the natural environment and do not rule out the capacity for more sophisticated strategies (Seed and Byrne 2010). In our task, subjects could have opted to focus on the cue they deemed to be most important (seemingly the puzzle-tube ends), and where there was a tie on this cue (if both ends were configured the same) they may have examined what they deemed to be the second most important cue (e.g. gap-size, see Fig. 2.5). Although this may seem contradictory as it still requires multiple cues to be examined, it nonetheless reduces the cognitive demands of the decision-maker as they are only ever considering a single cue at a time (Shah and Oppenheimer 2008). Mitchell et al. (2009) discuss the use of simulation- versus rule-based approaches in the development of passing false-belief tests in children, and suggest that in this context at least, simulation is the effortful default, with cognitively economical rules being derived from experience over time.

There was substantial between-subject variation in performance on this task, which makes it difficult to generalise about the cognitive mechanisms involved. Even if two individuals' performances were the same it is possible that one could have used heuristic rules to solve the task whereas the other used more abstract reasoning (Chittka and Jensen 2011).

However, differences in performance can prove revealing with regards to different strategies used. In a recent study investigating understanding of gravity and solidity in great apes Cacchione and Call (2010) found that different individuals used different strategies when searching for a reward, and not all individuals were able to change strategy flexibly. The use of different strategies may help to explain the differences in performance observed here, with Amos being the most flexible. Sandy may have acquired a correct rule over time, as her performance showed a general but non-significant trend of improvement across sessions (see Fig. 2.3). Silvia may have been using an incorrect rule (such as always moving the reward towards the closed end of the tube, which she did in 20 out of 32 trials where the ends were configured one open and one closed, see Fig. 2.5) which would have led to a systematic error within the subset of trials with the ends configured one open one closed, though her performance did not appear to correspond with any of the simulated performance outcomes (see Fig. 2.4). She did, however, self-correct in more trials than the other two subjects (20.5% of her incorrect trials), which may be indicative of a more 'planful' than 'planned' strategy, as was found to be the case for capuchin monkeys navigating 2D mazes (Pan et al. 2011). As a wild-caught orangutan, it is likely that Silvia's opportunities to gain learning experience in her early years were rather different to the other two subjects (born in captivity), which may have affected her problem-solving behaviour (Lethmate 1979). During a nine year study Galdikas (1982) found that ex-captive orangutans released into the wild exhibited tool-using behaviour in a much wider variety of contexts, compared with wild orangutans. Galdikas attributed this to differential learning experiences during critical learning periods before maturity (Galdikas 1982). Another point worthy of note regarding Silvia is that she was the most difficult subject to encourage to come to the apparatus (Tecwyn, personal observation), which may be indicative of her lower levels of motivation and attentiveness compared to the other subjects. It is interesting to note that the 9 year old subject performed best, as the four orangutans that solved trap-tube analogous tasks in other studies were all aged between 11-18 years, from a tested range of 6-33 years (Mulcahy and Call 2006b; Martin-Ordas et al. 2008). This study increases the

upper age tested to 44 years. It is possible that success in tasks of this nature may be related to age class, as younger orangutans are generally more exploratory of their habitat and its affordances, which is reflected in their larger locomotor repertoire (Thorpe and Crompton 2005; Thorpe and Crompton 2006), but a far larger dataset would be required to substantiate this.

In summary, our novel task improved on the methodological and procedural limitations of previous similar tasks and minimised the potential for associative learning across trials by presenting a deliberately limited number of trial-unique configurations. The design of our task did not permit unequivocal conclusions regarding the use of higher-level, deliberative processes to be drawn; rather our use of rule-simulations in the analyses demonstrated that successful subjects could have solved the task by using a combination of two procedural rules. GLMMs quantitatively supported the notion that the configuration of the puzzle-tube ends was used as a cue for choosing direction. This is nevertheless impressive, as performance did not improve significantly across sessions and Amos performed above chance-level in his initial session, suggesting that if these subjects were using a rule-based approach they must have already possessed some appropriate previously acquired causal knowledge (for example the inability of a reward to pass through barriers and possibly the size of a reward relative to a gap). Furthermore, the use of rules may in fact be a cognitively economical strategy compared with the use of deliberative processes for each trial (Shah and Oppenheimer 2008). Silvia may have been using an incorrect rule (e.g. move the reward towards the closed end), resulting in a systematic error that contributed to her poor performance, though previous experience, motivation and attention may have also played a key role.

Future studies should develop new paradigms to investigate the how tasks that require consideration of multiple steps prior to implementing actions are solved, with regards to cognitive strategies that subjects use. The focus should be on contexts in which animals are more likely to go beyond using simple strategies and tasks should be constructed in

such a way that success via the use of procedural rules is not possible. If the number of steps to be considered between initiation of actions and achieving the desired outcome could be systematically increased (which might be expected to increase cognitive demand (Wimpenny et al. 2009), a 'planning threshold' could theoretically be reached. It would be particularly interesting to compare the performance of a number of primate species on such tasks to generate a phylogenetic reconstruction of this cognitive ability and to begin to understand the socio-ecological challenges that may have driven its evolution. It is also imperative that future studies continue to attempt to tease apart alternative underlying cognitive mechanisms, with increased emphasis on detailed analyses of behaviour, as it seems that such studies with primates are now falling behind those conducted with birds (see e.g. Wimpenny et al. 2009; Cheke et al. 2011; Miyata et al. 2011).

This chapter has demonstrated that some at least some orangutans seem able to consider multiple obstacles when attempting to retrieve a reward from a puzzle-tube apparatus. However, success in this task was based on a binary choice, and post-hoc analyses revealed that it was possible to solve the task using a combination of procedural rules. Therefore, in the next chapter (chapter 3) I aim to address these issues with a novel piece of apparatus designed to test planning ability, where success is not based on a binary choice and subjects cannot always succeed by following procedural rules.

Chapter 3

A NOVEL TEST OF PLANNING ABILITY: GREAT APES CAN PLAN STEP-BY-STEP BUT NOT IN ADVANCE OF ACTION

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Abstract

The ability to identify an appropriate sequence of actions or to consider alternative possible action sequences might be particularly useful during problem-solving in the physical domain. We developed a new 'paddle-box' task to test the ability of different ape species to plan an appropriate sequence of physical actions (rotating paddles) to retrieve a reward from a goal location. The task had an adjustable difficulty level and was not dependent on species-specific behaviours (e.g. complex tool use). We investigated the planning abilities of captive orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) using the paddle-box. In experiment 1, subjects had to rotate one or two paddles before rotating the paddle with the reward on. Subjects of both species performed poorly, though orangutans rotated more non-food paddles, which may be related to their greater exploratory tendencies and bolder temperament compared with bonobos. In experiment 2 subjects could always rotate the paddle with the reward on first and still succeed, and most subjects of both species performed appropriate sequences of up to three paddle rotations to retrieve the reward. Poor performance in experiment 1 may have been related to subjects' difficulty in inhibiting the prepotent response to act on the reward immediately.

3.1 Introduction

Planning as an everyday concept has many connotations, and several terms are used more or less interchangeably to describe a myriad of behaviours that do not seem to have much in common (Parrila et al. 1996). At one end of the spectrum, planning can consist of anticipating the consequences of motor actions, for example grasping an object in an appropriate orientation (end-state comfort effect; Rosenbaum et al. 1990). This has been demonstrated to develop early in humans (by 19 months of age; McCarty et al. 1999) and also to have emerged early in primate phylogeny, being present in several lemur species (Chapman et al. 2010). At the other end of the spectrum lies episodic future thinking: the ability to mentally project oneself into an imagined future scenario (Suddendorf and Corballis 1997). There is continuing debate regarding which, if any, non-human species possess this latter capacity, with some researchers presenting experimental evidence for animals imagining and planning for future events (Mulcahy and Call 2006a; Raby et al. 2007; Osvath and Osvath 2008; Osvath 2009; Osvath and Karvonen 2012) and others arguing that foresight is an uniquely human ability (Suddendorf and Corballis 2007; Suddendorf et al. 2009). Clearly, these two examples of planning, and the multitude of intermediate cases, must pose very different cognitive demands and vary in terms of their information processing requirements (Chappell et al. 2012; Tecwyn et al. 2012).

Bearing this in mind, it is important to specify the type of planning that is of interest here, which is the type of planning that may be involved in problem-solving that is oriented towards current needs. This can be defined as the ability to identify an appropriate sequence of actions or consider alternative courses of action prior to execution (see Tecwyn et al. 2012 for further discussion). Behaviours exhibited by wild great apes that may involve this type of planning include the use of 'tool-sets' for extractive foraging of honey by chimpanzees (*Pan troglodytes*: Brewer and McGrew 1990); 'engineering' of alliances with the most profitable partners by bonobos (*Pan paniscus*; Hohmann and Fruth 2002; Aureli et al. 2008); hierarchical processing of plant material by gorillas (*Gorilla beringei*

beringei: Byrne et al. 2001) and gap-crossing in the compliant forest canopy by orangutans (*Pongo pygmaeus*: Chevalier-Skolnikoff et al. 1982).

How might planning for current needs be investigated experimentally? Several papers have advocated developing experimental methodologies and paradigms that consider different species' predispositions to allow testing of multiple species (Santos et al. 2006; Amici et al. 2010; MacLean et al. 2012), as at present systematic interspecific comparisons are still rare (Schmitt et al. 2012). This is important in order to avoid the presentation of tasks in an 'unfair' manner, hence biasing for or against the abilities of certain species (Roth and Dicke 2005). To date, studies investigating planning for current needs in non-human species have mostly fallen in to one of two categories: those involving the use of tools, and those involving computerised interfaces (but see e.g. Dunbar et al. 2005; Kuczaj et al. 2009; Miyata et al. 2011 for interesting alternative approaches).

Tool use studies of planning, usually focused on sequential tool use, or metatool use (e.g. Hihara 2003; Mulcahy et al. 2005; Taylor et al. 2007; Bird and Emery 2009; Wimpenny et al. 2009; Taylor et al. 2010; Martin-Ordas et al. 2012) have yielded many interesting insights. However, they may not be ideal when attempting to develop a comparative planning paradigm, for at least two reasons. First, they bias against non-tool-using species, as the behaviours involved in solving the task may not form part of their natural repertoire, and may require fairly precise manipulatory abilities (e.g. sufficient motor control to hold a stick and insert it into a narrow tube). Second, there is evidence to suggest that removing tool use from physical cognition problems can reduce cognitive load and improve performance (Seed et al. 2009b). Therefore, if it is planning rather than tool use that is the focus of study, it seems prudent to avoid the requirement for tool use.

Studies involving computerised environments have also been used to investigate planning ability. These require subjects to use either a touch-screen or joystick, for example to navigate through a two-dimensional maze (e.g. Fragaszy et al. 2003; Miyata and Fujita

2008; Fragaszy et al. 2009; Pan et al. 2011) or to recall a sequence of numbers (Biro and Matsuzawa 1999; Beran et al. 2004). Such techniques certainly have experimental advantages, such as precise timing of stimulus presentation and automatic recording of behavioural responses. However, they are expensive and time-consuming to implement, with subjects requiring extensive training to use the experimental apparatus prior to the start of testing. Furthermore, the physical and temporal distance between stimulus, response and reward, and the need for refined motor abilities can be problematic, particularly for younger individuals (Mandell and Sackett 2008).

A further problem with these and other cognitive tasks such as the trap-tube paradigm (Visalberghi and Limongelli 1994) is that initial errors made by the subject are often correctable. In trap-tube tasks for example, the reward can initially be moved in one direction, but the direction could be switched before the reward falls in a trap. Although error correction strategies can be enlightening (e.g. DeLoache et al. 1985), having the option of correcting an error may reduce the motivation of subjects to make the correct choice in the first place, or to plan for the correct solution (Tecwyn et al. 2012).

As well as considering the practical and paradigmatic issues raised above, it has been suggested recently by MacLean and colleagues (2012) that it would be fruitful for researchers to design tasks with an adjustable level of difficulty, in order to avoid the masking of meaningful variation due to floor or ceiling effects. In the case of planning during problem-solving, it would be useful to have a task that could distinguish between, for example, the ability to make selections between alternatives (proto-deliberative; Sloman 2010) and the ability to explore branching futures (fully deliberative; Sloman 2010), which differ in terms of their computational burden.

The aims of this study were two-fold. First, we aimed to design a new paradigm appropriate for comparative testing of planning ability in primate species (including humans) that:

- Did not involve complex tool use

- Did not depend on species-specific behaviours/competences
- Had an adjustable level of difficulty
- Did not have a performance outcome that was dependent on a binary choice, in order to reduce the possibility of the task being solved by chance
- Was not correctable, to encourage subjects to choose correctly initially
- Could be configured in a trial-unique manner, so the task had to be considered anew for each trial

Second, we aimed to use the new paradigm to investigate whether captive bonobos and orangutans (*Pongo pygmaeus*) are able to plan an appropriate sequence of actions (a) in advance (experiment 1); or (b) sequentially (experiment 2), in order to retrieve a food reward from a goal location. If the ability to plan was present in the great ape last common ancestor, then we might expect both bonobos and orangutans to exhibit planning behaviour. If it evolved more recently in an African ape ancestor, then we might expect only bonobos to perform well in our planning task. If on the other hand orangutans outperform bonobos, this may suggest that orangutans have refined their adaptations (both anatomical and cognitive) for arboreal living, beyond those that were present in the great ape common ancestor. As the only great ape species to remain in the terminal branch niche (Grand 1972) and therefore still face the locomotor demands as posited by Povinelli and Cant (1995), it seems feasible that orangutans have continued to face strong selection pressure for the ability to mentally 'try out' different possible courses of action, and may therefore potentially possess particularly refined planning skills.

3.2 Materials and methods

3.2.1 Subjects and housing

Four bonobos housed at Twycross Zoo, UK and eight orangutans housed at Apenheul Primate Park and Ouwehands Dierenpark Rhenen in the Netherlands, participated in this

study (Table 3.1).

Table 3.1 – Subjects that participated in the experiments reported in this study. C = captive born; W = wild born; Mo = mother-reared; H = hand-reared

Species	Subject	Sex	Age	Birthplace	Rearing	Location	Experiment participation
Bonobo	Cheka	F	15	C	Mo	Twycross	1,2
Bonobo	Keke	M	17	C	Mo	Twycross	1,2
Bonobo	Banya	F	21	C	Mo	Twycross	1
Bonobo	Kichele	F	22	C	Mo	Twycross	1,2
Orangutan	Amos	M	11	C	Mo	Apenheul	1,2
Orangutan	Sandy	F	29	C	Mo	Apenheul	1,2
Orangutan	Radja	F	~49	W	Mo	Apenheul	1
Orangutan	Jingga	M	4	C	Mo	Ouwehands	2
Orangutan	Yuno	M	5	C	Mo	Ouwehands	2
Orangutan	Jewel	F	~27	W	Mo	Ouwehands	1,2
Orangutan	Tjintah	F	28	C	Mo	Ouwehands	2
Orangutan	Anak	F	36	C	H	Ouwehands	1,2

Not all subjects participated in all of the experiments, and in some experiments the number of trials completed varied between subjects. This was to comply with zoo-specific regulations relating to research. Details of which individuals participated in which experiments are given in Table 3.1 as well as the separate methods sections for each experiment below. The number of trials completed by different individuals is specified in the relevant sections. Bonobos at Twycross and orangutans at Ouwehands were naive with respect to cognitive testing, whereas orangutans at Apenheul had previously been exposed to a trap-tube type task reported in Tecwyn et al. (2012; chapter 2 of this thesis). The apes at all three institutions were managed with an attempt to simulate fission-fusion societies, so composition of the groups in the different sub-enclosures changed on a regular basis. Enclosures at all zoos were equipped with climbing elements including tree trunks, fibreglass poles, ropes, netting, shelves, platforms and enrichment materials.

3.2.2 Apparatus: the paddle-box

The paddle-box apparatus was attached to the outside of the enclosures and consisted of an opaque Perspex box (60 cm x 60 cm x 6 cm) containing eight rotatable paddles (14.5 cm x 3.5 cm x 1.7 cm; 1-8 in Fig. 3.1a) on three levels (i-iii in Fig. 3.1a). There were four possible goal locations (each measuring 11 cm x 4.5 cm x 4.5 cm; A-D in Fig. 3.1a) at the base of the apparatus that could all either be open or blocked.

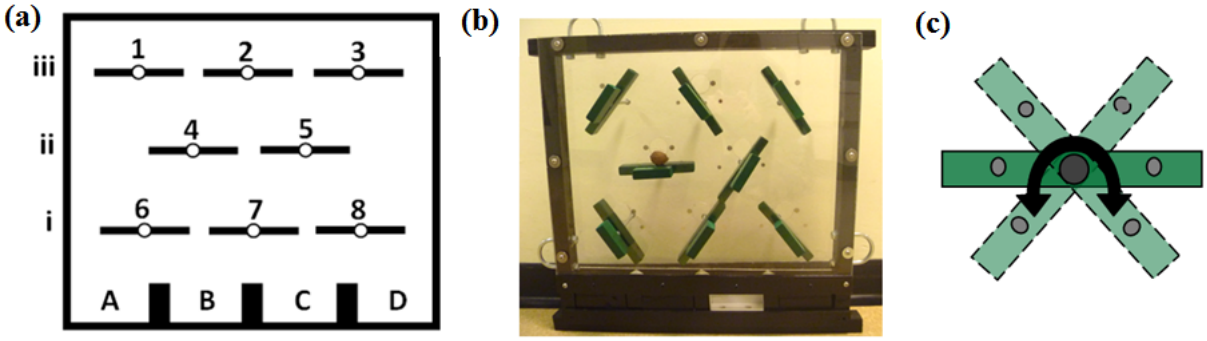

Figure 3.1 – (a) Schematic depiction of the paddle box apparatus from the test subject's viewpoint showing the paddles (1-8), levels (i-iii) and goal locations (A-D); (b) photograph of the apparatus showing the reward on paddle 4 (level ii) and the open goal location in position C, with the other three goals blocked; and (c) diagram of the paddle mechanism, illustrating the three positions in which the paddles could be held by magnets (flat; diagonal left; diagonal right)

The paddle-box was designed to be mechanically accessible to any animal capable of operating the simple paddle mechanism, making it ideal for comparative testing of a number of species, including non-tool users. The paddles were rotated by subjects using wooden handles (7cm x 2.5cm x 1.7cm) that extended out of the front of the box and were oriented parallel to the paddles inside the box (see Fig. 3.1b). The handles could be operated in a number of ways; for example by pushing down from above or up from underneath at either end of a handle, or by using a twisting action. They were designed to be large enough so they did not require fine motor control and thus reduce the chance of subjects accidentally turning them the wrong way. Once a paddle was rotated, directional choices were not easily correctable because the reward rolled quickly off the paddle. The experimenter (ECT) could quickly and safely configure the paddle-box between trials by

rotating paddles using long rods that extended out of the back of the box. Each paddle could be set up in one of three orientations (flat; diagonal left; diagonal right, see Fig. 3.1b for examples of these orientations). Paddles were held in position by weak magnets (Fig. 3.1c) so that they were easily rotatable by the subjects, but a moving reward did not displace them from their orientation.

3.2.3 General procedure

The experimental procedure varied between institutions in order to comply with the different zoos' regulations. All subjects were tested in off-show rooms (10-22 m^2) where they were held regularly for feeding and during cleaning of the main enclosures. The bonobos at Twycross were not isolated for testing (in compliance with the institution's ethical guidelines), and consequently session length and the number of trials completed varied between individuals. Usually however, a single bonobo monopolized the apparatus during testing (though the individual varied between testing sessions), and minimal competition for the apparatus was observed. Orangutans were tested in isolation apart from Sandy who was accompanied by two dependent juveniles. Subjects were not food deprived before the trials, water was available ad libitum and they could choose to stop participating at any time. The food reward in each trial was a small piece of fruit (orange, apple, pear) or bread and subjects remained motivated to obtain the rewards throughout the study. Due to constraints imposed by the testing area dimensions, the paddle-box was presented to orangutans at ground-level, whereas for bonobos it was attached to the enclosure at a height of approximately 1.5 m (from the base of the paddle-box to the ground).

3.2.4 Familiarisation

There was a minimal familiarisation phase to confirm the ability of subjects to retrieve a reward from an open goal location. Each subject was presented with the apparatus with goals B and C open and A and D blocked, and the reward starting on paddle 7 (see

Fig. 3.1a). Subjects could retrieve the reward by rotating paddle 7 in either direction and extracting the reward from one of the open goals. Once subjects had succeeded in retrieving the reward five times, they were able to progress to the testing phase. None of the subjects experienced the reward becoming trapped during familiarisation. All subjects except for one achieved the familiarisation criterion within a few minutes of first encountering the apparatus. One orangutan (Jewel) did not rotate the paddle with the reward on within a few minutes, so the experimenter demonstrated the rotation action to her. She subsequently succeeded in reaching the criterion for progressing to the testing phase.

3.2.5 Testing phase

Two experiments were carried out, each described in greater detail below. In both experiments, the reward could start on any paddle excluding paddles 1 and 3 (see Fig. 3.1a). The reason for this was that if paddles 1 or 3 were rotated towards the outer edge of the paddle-box, the reward could simply drop down to the bottom of the apparatus, missing out the paddles on the middle level. The minimum number of steps required to retrieve the reward in any given trial ranged from one to three and was pseudorandomised within each block, with the constraint that no more than two trials with the same number of minimum moves occurred consecutively. The paddle that the reward started on (the start paddle) and the level on which it was located (i-iii in Fig. 3.1a) were also pseudorandomised such that they were not the same in more than two consecutive trials. In all trials only one goal location was open and the other three were blocked. The open goal was white and visually distinct from the blocked goals that were black (see Fig. 3.1b). If the reward was successfully navigated to the open goal location it could be retrieved by the test subject from the front of the apparatus. If the reward became trapped at one of the blocked goal locations it could not be accessed by the subject and was removed from the back of the apparatus by the experimenter. For some trials it was possible to retrieve the reward in the minimum number of steps in multiple ways (a maximum of three), that is, there was

more than one viable route from the start paddle to the open goal location. Impossible configurations, in which the reward could not be moved from the start paddle to the goal via any sequence of paddle rotations (e.g. reward starting on paddle 4 and open goal in location D, see Fig. 3.1a) were never presented.

3.2.6 Data scoring and analysis

All trials were videotaped. For each trial, whether the reward was retrieved from the open goal location (correct) or became trapped (incorrect) was scored. In some trials, for example if a paddle was rotated very rapidly, the reward did not follow the path of the pre-positioned non-food paddles and ended up in an unexpected goal location, i.e. subjects were not rewarded when they should have been, or vice versa. If the reward ended up in a blocked goal location when the paddles were configured so that it should have ended up in the open goal it was scored as an 'unexpected trapping'. Conversely, if it ended up in the open goal location in this way it was scored as an 'unexpected retrieval'. In cases where a reward was 'unexpectedly trapped' despite the subject performing a valid sequence of paddle rotations, this was scored as correct. If a reward was 'unexpectedly retrieved' in this manner it was scored as incorrect. Information regarding each individual paddle rotation was also recorded. Specifically:

- paddle identity (1-8 in Fig. 3.1a)
- whether it was the start paddle (paddle on which the reward started, e.g. paddle 4 in Fig. 3.1b) or a non-food paddle (all other paddles)
- direction of rotation:
  - left or right
  - towards or away from open goal location (this information was not recorded for trials in which the start paddle was located directly above the open goal location, as was the case for start paddle 4 and goal B, and start paddle 5 and goal C, see Fig. 3.1a).

- Non-food paddles that were rotated were further classified according to:
  - whether they were relevant (rotation enabled the reward to be retrieved, e.g. paddle 7 in Fig. 3.1b) or irrelevant (did not need to be rotated for the reward to be retrieved)
  - the level on which they were located, relative to the level of the start paddle (same level; above; below)
  - timing of rotation (pre-reward insertion; whilst the reward was on the start paddle; after the reward had become trapped)

A second observer (JC) independently scored 20% of the trials. Inter-observer reliability was calculated using Cohen's kappa (k), and was excellent for all of the variables scored (experiment 1: k ranged from 0.90 (direction of start paddle rotation relative to goal location) to 0.98 (reward retrieval); experiment 2: k=0.89 for reward retrieval and 0.98 for direction of start paddle rotation (left or right)). Data were analysed using PASW Statistics 18 (IBM SPSS Inc. 2009) and R 2.11.1 (LME4 package, R Development Core Team 2010).

3.3 Experiment 1: advance planning task

This task was presented first as it was considered to be the most difficult in terms of planning demands. Presenting an easier task first could potentially train subjects to succeed in a more difficult task, which we wanted to avoid.

3.3.1 Methods

All four bonobos and five orangutans (Amos, Jewel, Sandy, Anak and Radja) participated in experiment 1. Subjects were presented with up to 12 blocks of 12 trials. The total number of trials completed by each subject depended on two factors: a subject's availability for testing, and their performance in the first eight blocks. If a subject successfully solved any 2- or 3-step trials then they were presented with up to four additional blocks. This

was because subjects that succeeded in this initial testing period through planning their actions might have been expected to show repeated success with additional testing, and we wanted to maximize the chance for subjects to display the ability to succeed at the task, should it exist. Table 3.2 gives details of the number of trials completed by each subject.

3.3.2 Paddle-box configurations

Within a block, each trial was a unique configuration of the paddle-box apparatus requiring a minimum of one, two or three paddle rotations to retrieve the reward. In 1-step trials the reward could start on any of the three levels (i-iii in Fig. 3.1a); in 2-step trials the reward either started on the middle or top level; and in 3-step trials the reward could only start on the top level. In 2- and 3-step trials subjects had to pre-position one or two non-food paddles before rotating the start paddle (see Fig. 3.2a for an example of a 2-step trial). Pseudorandomisation occurred as described in section 3.2.3. The open goal location was fixed within a block but changed between blocks. In each trial, only the start paddle was positioned in the flat orientation. All of the other paddles were positioned in one of the two possible diagonal orientations (Fig. 3.2a; see also Fig. 3.1b). This meant that if the start paddle was rotated first, the reward would slide down to the bottom of the apparatus and end up at one of the blocked goal locations (Fig. 3.2a; see also Fig. 3.1b).

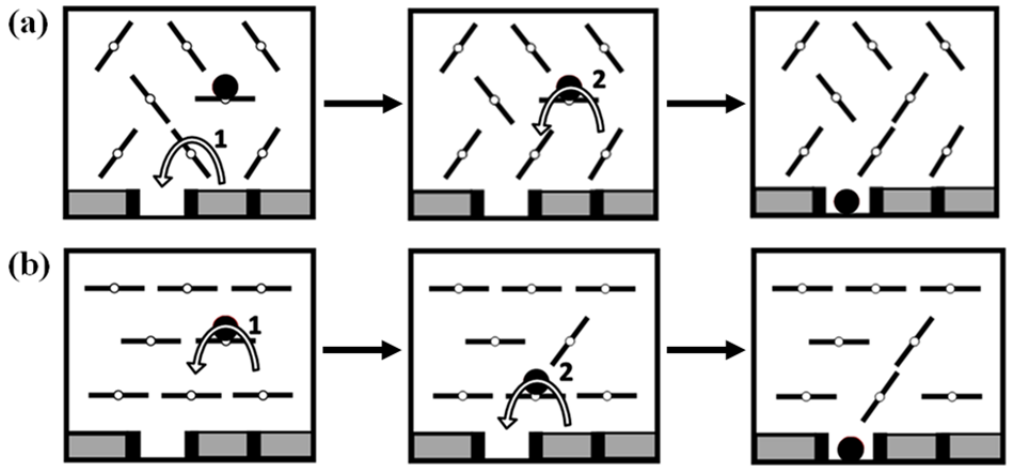

Figure 3.2 – Schematic examples of how to solve (a) a 2-step advance planning trial (experiment 1) and (b) a 2-step sequential planning trial (experiment 2) in the minimum number of moves

3.3.3 Results

The number of trials completed ranged from 43 to 120 (Table 3.2). In 8.0% of all trials the reward was unexpectedly retrieved and 2.0% of trials resulted in an unexpected trapping. Most unexpected retrievals occurred when the start paddle was located directly above a goal location and the subject rotated it very rapidly, causing the reward to fall between the two paddles beneath and into the open goal location, rather than sliding down either one of them and becoming trapped. The number of 1-, 2- and 3-step trials in which the reward was correctly retrieved by each subject is shown in Table 3.2, together with the total number of trials completed by each subject and their first trial performance for each trial-type.

Table 3.2 – Results of experiment 1 (advance planning) and experiment 2 (sequential planning). Number of trials correct and the number completed, and first trial performance for each trial-type (1-step, 2-step, 3-step). C = correct first trial; I = incorrect first trial; - = did not participate

Species	Subject	No. trials correct / no. trials completed; 1st trial performance					
		Experiment 1: advance			Experiment 2: sequential		
		1-step	2-step	3-step	1-step	2-step	3-step
Bonobo	Cheka	15/28; C	0/35; I	0/28; I	15/18; C	16/18; C	14/19; C
Bonobo	Keke	9/21; C	0/23; I	0/12; I	19/20; C	14/20; C	17/20; C
Bonobo	Banya	10/13; C	0/20; I	0/10; I	-	-	-
Bonobo	Kichele	13/27; C	0/33; I	0/33; I	8/14; C	7/12; C	6/12; I
Orangutan	Amos	24/38; C	2/43; I	0/29; I	13/16; C	15/16; C	13/16; C
Orangutan	Sandy	25/40; C	3/46; I	0/34; I	16/16; C	12/16; C	12/16; C
Orangutan	Radja	7/18; C	2/21; I	0/11; I	-	-	-
Orangutan	Jingga	-	-	-	12/16; I	7/16; C	7/16; I
Orangutan	Yuno	-	-	-	16/16; C	16/16; C	15/16; C
Orangutan	Jewel	14/28; I	0/29; I	0/23; I	15/16; C	11/16; C	11/16; C
Orangutan	Tjintah	-	-	-	14/16; I	10/16; C	12/16; I
Orangutan	Anak	22/38; C	0/43; I	0/29; I	15/16; C	8/16; C	10/16; C

In the majority of trials (84.9% for orangutans and 98.3% for bonobos) only the start paddle was rotated. Based on a subject only rotating the start paddle in a trial, the

probability of success in a 1-step trial was 0.5, because one of the two possible directions in which the paddle could be rotated resulted in the reward ending up in the open goal, whereas the other direction led to it becoming trapped). Only Amos (orangutan) performed significantly better than expected by chance (based on a 0.5 probability of success) across the 1-step trials he completed (Table 3.2; binomial test: 24/38 trials correct, p=0.03). Even within the subset of 1-step trials in which the reward started on the bottom level, again only Amos' performance was above chance-level (binomial test: 16/20 trials correct, p=0.01).

Most of the subjects did not solve any of the 2- or 3-step trials in which one or two non-food paddles had to be pre-positioned before rotating the start paddle (Table 3.2). Three orangutans (Amos, Sandy and Radja) did retrieve the reward in some 2-step trials (see Table 3.2) and they did this by pre-positioning relevant non-food paddles in advance of rotating the start paddle.

Start paddle rotations

Two orangutans and one bonobo exhibited a significant tendency to rotate the start paddle to the right (binomial test: Anak: 82/110, p<0.001; Jewel: 50/80, p=0.034; Cheka: 62/91, p=0.001) and one bonobo tended to rotate the start paddle to the left (binomial test: Kichele: 66/96, p<0.001). The remaining subjects did not exhibit a directional preference.

Fig. 3.3 shows that four out of five orangutans but no bonobos rotated the start paddle towards the open goal location significantly more often than expected by chance.

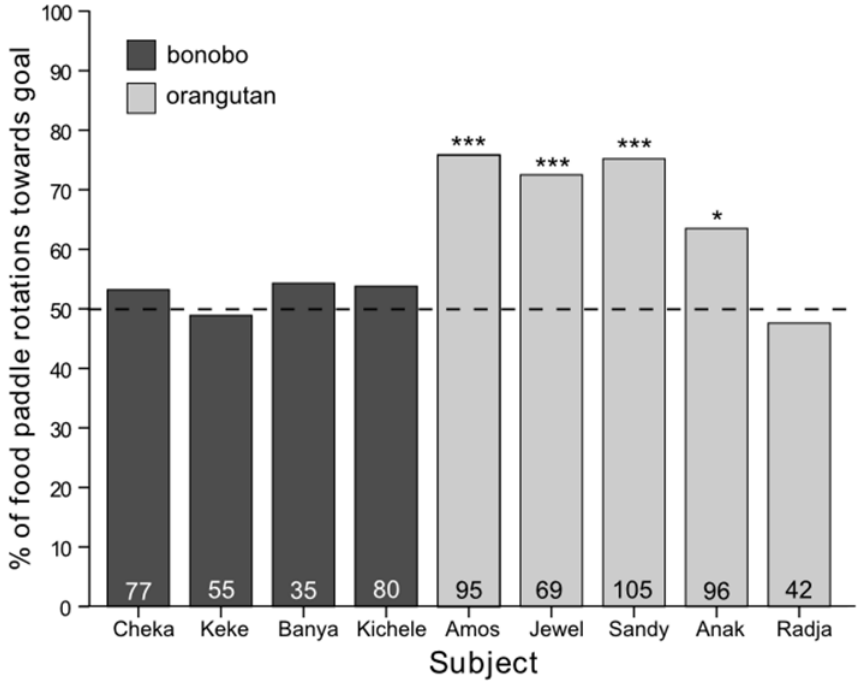

Figure 3.3 – Percentage of start paddles rotated towards (as opposed to away from) the goal location by each subject in experiment 1. Numbers at the base of bars indicate the total number of trials that each subject participated in that were included in this analysis. * indicates $p<0.05$ and *** indicates $p<0.001$ in a binomial test

In some trials the start paddle was located directly above the open goal location; hence it could not be turned towards or away from the goal. Within this subset of trials, each of the four orangutans that preferentially rotated the start paddle towards the open goal location in the above analysis (Fig. 3.3) rotated the start paddle in a random direction (binomial test: $p>0.05$ for all).

Non-food paddle rotations

All of the orangutan subjects and two out of four bonobos rotated at least one non-food paddle during the experiment. The total frequency of non-food paddle rotations for all trials ranged from zero (Cheka and Keke) to 43 (Anak). Fig. 3.4 shows that orangutans rotated more non-food paddles (both relevant and irrelevant) than bonobos. Orangutans did not however rotate significantly more relevant than irrelevant non-food paddles (Fig. 3.4; Mann-Whitney U Test: $N_1=48$, $N_2=47$, $p=1.000$).

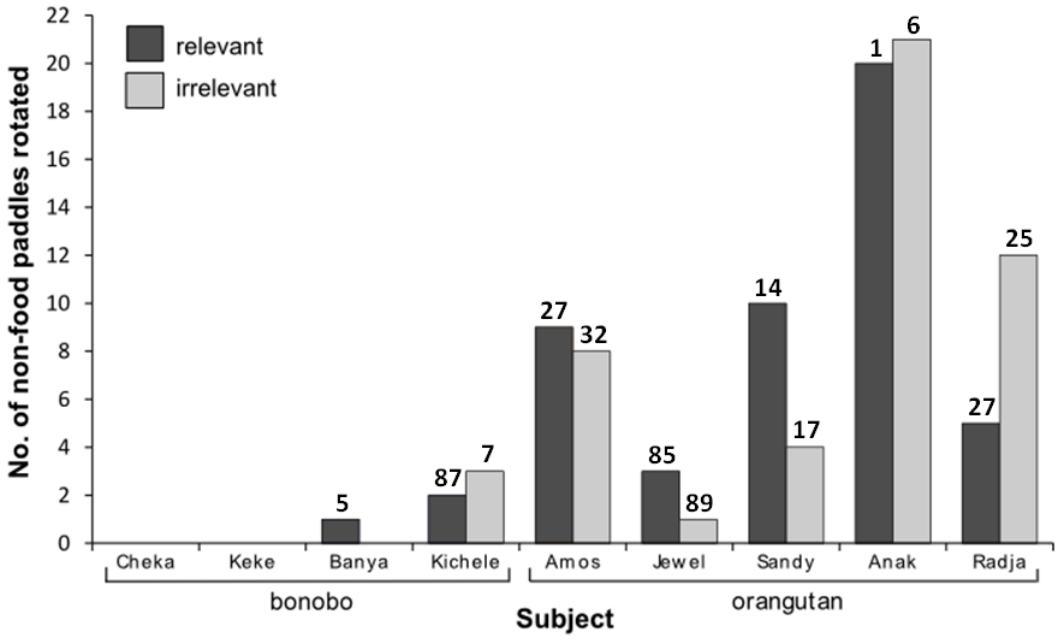

Figure 3.4 – Total number of relevant and irrelevant non-food paddles rotated by each subject across all trials in experiment 1. Numbers above the bars indicate the number of the trial in which rotation of a relevant or irrelevant non-food paddle first occurred

For subjects that rotated relevant non-food paddles, the first trial in which this occurred ranged from trial 1 (Anak) to trial 87 (Kichele; see numbers above bars in Fig. 3.4). Of the six subjects that rotated both relevant and irrelevant non-food paddles, four rotated a relevant paddle in an earlier trial than they rotated an irrelevant paddle (Fig. 3.4).

All subjects that rotated non-food paddles rotated more that were located below the starting level of the reward as opposed to on the same level or above. Overall, 75.3% of all non-food paddles rotated were below the level of the start paddle.

3.3.4 Discussion

Subjects generally failed at this task, even in 1-step trials (Table 3.2). In 93.1% of trials only the start paddle was rotated, so subjects rarely pre-positioned any non-food paddles, which was necessary for success in the 2- and 3-step trials. Three orangutans succeeded in some 2-step trials by pre-positioning relevant non-food paddles (Table 3.2). Although this may give an impression of an 'understanding' of the task in these particular trials, overall

there was no significant difference between the number of relevant and irrelevant paddles rotated (Fig. 3.4), suggesting that subjects may simply have been rotating paddles at random. The position of the non-food paddles they did rotate (most frequently on levels below the start paddle) may however indicate that subjects were aware that paddles higher up in the apparatus were less likely to influence the path of the reward because the reward only ever moved down towards the bottom of the paddle-box. Bonobos very rarely rotated any non-food paddles (Fig. 3.4). However, the observed difference in propensity to rotate non-food paddles may reflect a difference in the two species' exploratory tendencies and temperament (Herrmann et al. 2011), or variation in testing conditions, rather than any difference in cognitive ability.

Although subjects generally only rotated the start paddle, four out of five orangutans (but no bonobos) did preferentially rotate the start paddle towards the open goal location (Fig. 3.3). Furthermore, in trials where the start paddle was directly above the goal, these same subjects turned the paddle in a random direction. While turning the start paddle towards the open goal did not enable subjects to succeed in the task, it suggests that they may at least have encoded information about the relevance of the open goal for retrieving the reward, and turned the start paddle so that the reward moved towards it. Subjects that did not preferentially rotate the start paddle towards the open goal may not have encoded the relevance of the open goal location, despite the fact that it was visually and haptically distinct from the blocked goal locations (see Figure 3.1b). It is also possible that these subjects may have exhibited this behavior, had they been given a small amount of pre-training so that they learned about how the reward moved depending on which way the start paddle was rotated. However, as there was no evidence for improvement in performance across sessions this is perhaps unlikely.

The failure in 2- and 3-step trials of subjects that apparently encoded the relevance of the goal location could either have stemmed from a lack of understanding of how non-food paddles affected the path of the reward, or their inability to inhibit the prepotent response

to rotate the paddle with the food on (i.e. the start paddle). Reaching directly for a desirable object is known to be a prepotent response, the prevention of which requires the ability to reject some alternative (inappropriate) actions and favour others (Diamond 1990). The salience of the food reward on the start paddle may have meant that subjects were unable to divert their attention to other relevant aspects of the apparatus (i.e. the positions of the non-food paddles) (Vlamings et al. 2010). Food salience is known to affect the performance of several primate species in reversed contingency tasks, where subjects are presented with a choice between a small and a large quantity of food, but they receive the opposite of what they select (Boysen and Berntson 1995). In the delay of gratification test on the other hand, apes have accumulated food items for several minutes before taking the rewards (e.g. Beran et al. 2012).

It is unclear what caused the subjects that seemingly encoded the relevance of the goal location to fail at this task. Possibilities included: (1) an inability to plan an appropriate sequence of actions, (2) an inhibitory control problem, and (3) a lack of understanding of how diagonally positioned non-food paddles influence the path of the reward. In the second experiment we eliminated the two latter possibilities to determine whether this improved subjects' ability to plan in the task.

3.4 Experiment 2: sequential planning task

3.4.1 Methods

Three bonobos (Cheka, Keke and Kichele) and seven orangutans (Jingga, Yuno, Amos, Jewel, Tjintah, Sandy and Anak) participated in experiment 2 (Table 3.1). Jingga, Yuno and Tjintah had not participated in experiment 1 and so had no previous experience with the apparatus apart from the familiarisation phase. All seven orangutan subjects were presented with four blocks of 12 trials (one block with the open goal in each of the four possible locations); the number of trials completed by the bonobos varied between subjects

(Cheka: 55, Keke: 60, Kichele: 37).

3.4.2 Paddle-box configurations

In this experiment, all of the paddles were set up in a flat orientation at the start of each trial. The number of steps required to solve each trial was dictated by the level on which the reward started. As in experiment 1, all trials could be solved in one, two or three steps. The key difference here was that all trials could be solved by rotating the start paddle first, and then by rotating paddles on which the food was subsequently located, so subjects never had to pre-position non-food paddles. An example of how to retrieve the reward in a 2-step sequential trial is shown in Fig. 3.2b. In this trial there was only one correct route from the start paddle to the open goal location. However, in several of the 2- and 3-step trials the reward could be retrieved by taking a number of different routes. As in experiment 1 the start paddle and number of steps required to retrieve the reward (i.e. the start level) were pseudorandomised within each block. The open goal location was fixed within a block but changed between blocks.

3.4.3 Results

Overall performance ranged from 54.1% (Kichele) to 97.9% (Yuno) of trials correct (see Table 3.2 for individual performance in different trial-types). However, because the probability of success varied between different trial-types, it was not possible to conclude whether or not individual subjects' overall performances were better than expected by chance. Therefore, five different trial-types were identified, the probability of success for each was calculated, and each subject's performance within each trial-type was assessed.

Performance in different trial-types

In all 1-step trials there was a 50% chance of success, based on the start paddle being rotated immediately (as was the case in experiment 1). The 2-step trials could be classified

as those for which there was only one solution (i.e. only one possible route from start paddle to goal, as in Fig. 2b), and those for which there were two solutions (two viable routes from start paddle to goal). Similarly, 3-step trials could be split into those with only one solution, and those with three viable solutions.

It was possible to calculate the probability of retrieving the reward by chance in each of these 2- and 3-step trial-types based on the premise that subjects always rotated the paddle on which the food was located at any given point in a random direction. For example, to solve the 2-step trial in Fig. 3.2b (where there is only one valid route to the goal) the subject had to rotate the start paddle to the left (step 1 in Fig. 3.2b), then rotate the bottom centre paddle to the left (step 2 in Fig. 3.2b). The probability of this sequence occurring was 0.5 * 0.5 = 0.25. Therefore, for this trial-type there was a 25% chance of the reward being retrieved by chance. Having calculated probabilities of success for the different trial-types (see Appendix B1 for additional details), it was possible to examine subjects' individual performances using binomial tests, the results of which are shown in Fig. 3.5 (see Appendix B2 for individual binomial test results).

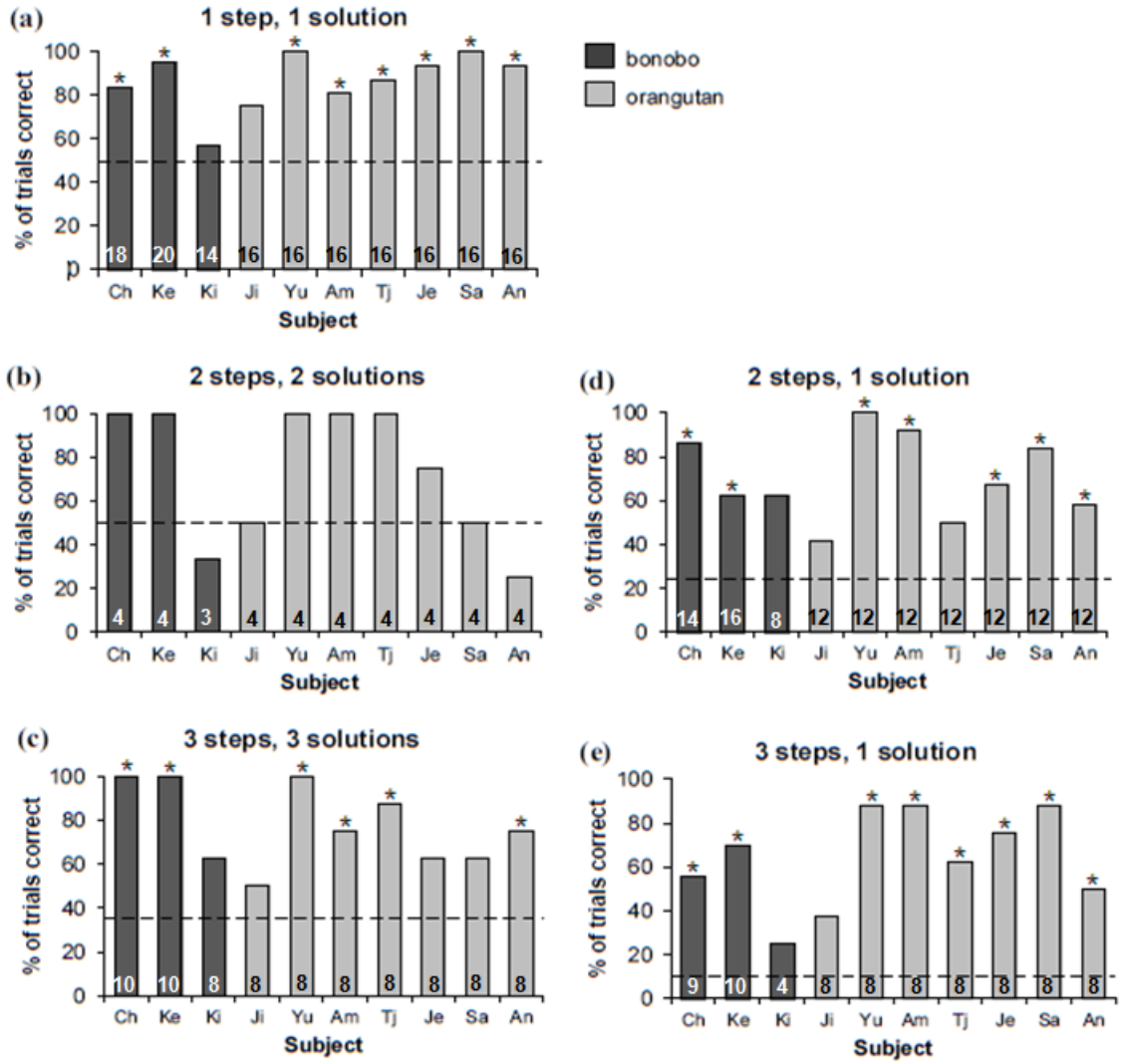

Figure 3.5 – Percentage of trials correct for each subject (Ch=Cheka, Ke=Keke, Ki=Kichele, Ji=Jingga, Yu=Yuno, Am=Amos, Tj=Tjintah, Je=Jewel, Sa=Sandy, An=Anak) within the five different trial-types in experiment 2. Numbers at the base of bars indicate the total number of trials of this type in which the subject participated. Dashed lines indicate the percent chance of retrieving the reward if the start paddle and subsequent paddles on which the food was located were rotated in a random direction: (a): 50%; (b): 50%; (c): 37.5%; (d): 25%; (e): 12.5%. * indicates $p<0.05$ in a binomial test. Binomial tests were not run for (b) because the maximum number of trials completed by a subject was 4, but the graph is shown for completeness

Binomial tests were not used to assess performance in the 2 steps, 2 solutions trials (Fig. 3.5b), because the maximum number of trials of this type completed by a subject was four.

One bonobo (Kichele) and one orangutan (Jingga) did not perform better than expected

by chance in any of the trial-types (Fig. 3.5). Three orangutans (Yuno, Amos and Anak) and two bonobos (Cheka and Keke) performed better than expected by chance in all of the trial-types for which binomial tests were run (Fig. 3.5). The remaining three orangutans all performed above chance-level in all but one trial type; Tjintah did not reach criterion in the 2 steps, 1 solution trial-type (Fig. 3.5d) and Jewel and Sandy failed in the 3 steps, 3 solutions trial-type (Fig. 3.5c).

Jingga, who was unsuccessful across all trial-types, was the only subject to improve his performance across testing blocks. In block 1 he retrieved the reward in 42% of trials, compared with a 75% success rate in his last block (Friedman test: $\chi^2{}_1$=4.0, p=0.046).

None of the subjects exhibited significant directional preferences when rotating the start paddle (binomial tests: p>0.05 for all). This includes the three subjects that did exhibit directional preferences in experiment 1.

Two out of three orangutans (Jingga and Yuno) subsequently succeeded in an additional version of this task, in which the goal location was switched between trials within each block, as opposed to only between blocks (Appendix B3). Unfortunately it was not possible to test any additional subjects in this version of the task, due to safety concerns associated with the proximity between the experimenter and subject that was necessary to switch the goal location between trials.

Factors associated with success

To explore the factors related to success in experiment 2, we fitted a generalized linear mixed model (GLMM) with binomial error distribution, using correct or incorrect sequence of paddle rotations as a binary response. We began by entering all probable explanatory terms and possible two-way interactions between them. The start-level of the reward, the location of the open goal, species and sex were included as fixed factors, as well as start-level x goal location as an interaction term. Subject was included as a random

factor on the intercept, and trial number as a random effect on the slope (Crawley 2007). Terms were sequentially dropped from the model until the minimal model contained only terms whose elimination would significantly reduce the explanatory power of the model (Thornton and Samson 2012).

The full model (AIC=491.3) showed that the start-level of the reward influenced the likelihood of subjects performing a correct sequence of paddle rotations (and hence retrieving the reward). Dropping the interaction term (start-level x goal location) significantly reduced the explanatory power of the model (likelihood ratio test comparing the two models: χ^2_6=21.86, p=0.0013) so this term was retained. Neither sex nor species significantly affected success, so these terms were dropped from the model. Trial number explained little variance in the model; indicating that the subjects did not improve over the course of the experiment (Crawley 2007). The minimal model (AIC=488.7) did not significantly differ from the full model in terms of explanatory power (χ^2_4=5.38, p=0.25). Post-hoc Tukey tests were used to investigate pairwise comparisons between the different start-levels. There was a significant difference in performance when the reward started on level 1 compared with level 3 (Z=3 .217, p=0.004), but no difference between levels 1 and 2 or 2 and 3.

3.4.4 Discussion

Most subjects performed well in this task. Only one orangutan and one bonobo failed to perform better than expected by chance across any trial-type (Fig. 3.5), but the orangutan (Jingga) did improve significantly across testing blocks. These results suggest that in this experiment, the majority of subjects encoded the relevance of the open goal location and were able to plan an appropriate sequence of paddle rotations to retrieve the reward, or learned to do so during the experiment. It is particularly noteworthy that Yuno and Tjintah were successful given that they did not participate in experiment 1, implying that previous experience with the apparatus was not required for success in this task.

The GLMM results and Fig. 3.5 show that when the reward started on the top level subjects were significantly less likely to retrieve the reward compared with when it started on the bottom level. This is what would be expected if the number of steps that must be considered increases cognitive demand, as was found to be the case in sequential tool use experiments with New Caledonian crows (*Corvus moneduloides*: Wimpenny et al. 2009) and great apes (Martin-Ordas et al. 2012). Interestingly, more subjects performed better than expected by chance in the 3 steps, 1 solution trials (12.5% chance of success) than in the than 3 steps, 3 solutions trials (37.5% chance of success). In the 3 steps, 1 solution trials, the goal had to be located prior to rotating the start paddle, because if the direction of this first rotation was incorrect then the reward was subsequently impossible to retrieve. However, because the goal was always in position A or D (see Fig. 3.1a) for these trials, subjects could succeed by using the rule 'rotate paddle with food on towards the open goal'. Also, in the 3 steps, 3 solutions trials the paddles had to be rotated in different directions, whereas in the 3 steps, 1 solution trials every paddle had to be rotated in the same direction, which may have been less challenging from a motor control perspective.

3.5 General discussion

Using a new paradigm (the paddle-box) we were able to manipulate the demands involved in a physical planning task in which subjects had to retrieve a food reward from an open goal location. By designing an apparatus that is simple to operate, does not require complex tool use and has an adjustable level of difficulty, we feel that we have gone some way to developing a test of planning ability appropriate for a range of species.

What evidence for planning?

Overall, subjects failed in experiment 1 but succeeded in experiment 2, though there was substantial inter-individual variation in performance in both experiments. Although both experiments in this study required subjects to select between multiple possible sequences of

actions, experiment 1 posed more complex information processing demands than experiment 2. As well as needing to encode information regarding how the diagonally positioned non-food paddles would influence the path between the reward's starting position and the goal, in 2- and 3-step trials subjects had to inhibit the prepotent response to turn the start paddle with the reward on immediately. In experiment 2 on the other hand, trials could be solved by always turning the paddle with the reward on first, because all of the paddles were in a flat orientation. This permitted the task to be solved in a more step-by-step manner, because the position of the reward relative to the goal location could be reassessed at each level.

The fact that subjects of both species could retrieve the reward when they were able to plan in a step-by-step manner (experiment 2) suggests that they did encode relevant task features such as the relevance of the open goal. The success of two orangutans (Yuno and Tjintah) in experiment 2 without having participated in experiment 1 also demonstrated that prior experience with the apparatus was not a prerequisite for success in this task; rather experiment 2 was (as predicted) an easier task. Successful performance of most subjects in experiment 2 is in keeping with the 'one-element planning' demonstrated by chimpanzees during 2D maze navigation, where subjects made decisions at each choice point on the basis of one property (e.g. Euclidean direction to the goal; Fragaszy et al. 2003). However, in the 2- and 3-step trials that only had one possible solution in experiment 2 of our study, the initial paddle rotation had to be in the correct direction, otherwise the reward would have ended up in a location from which its retrieval was impossible. Therefore, in these trials, subjects had to plan their first move based on where the goal was located. Furthermore, in trials in experiment 2 where there were multiple possible correct sequences of action, orangutans solved them in a flexible manner, utilising different routes from a given start paddle to a goal, sometimes turning the start paddle away from the Euclidean direction to the goal (Tecwyn, personal observation). This suggests that they did not simply rely on a procedural rule based on turning paddles towards the goal.

Orangutans and bonobos have previously exhibited planning skills in captive experiments. Martin-Ordas et al. (2012) recently demonstrated that all four species of great ape are able to use up to five tools in sequence to retrieve a reward. Both species have also been found to be capable of saving tools for future use (Mulcahy and Call 2006a). The results of experiment 2 in this study provide evidence of the ability of captive orangutans and bonobos to plan an appropriate sequence of actions outside of a complex tool-using context.

Interspecific differences in paddle-box performance?

Unfortunately it was not possible to draw direct comparisons between the performances of the two species due to unavoidable methodological differences, particularly those concerning whether the subjects were tested individually or in a group. Generally speaking, individuals that are able to concentrate and are not distracted will perform better in cognitive tasks (Herrmann and Call 2012), and attention is known to be important in planning tasks (Parrila et al. 1996). While orangutans were tested individually (apart from those with dependent infants or juveniles), bonobos were tested in their social groups. This may have disrupted their attention, and prevented them from perceiving and encoding relevant task features. Conspecifics could have attempted to steal the rewards, which may have introduced a competitive element and encouraged impulsive behaviour, depending on which other individuals were present (Stevens and Stephens 2002). There was also the potential for subjects in the same subgroup (Keke, Banya and Kichele) to learn to solve the tasks through observation, but we found no evidence for this.

However, some differences between orangutans and bonobos were apparent in experiment 1, which when taken together with the findings of other experimental work warrant further investigation. Although neither species succeeded in experiment 1, four orangutans but no bonobos preferentially rotated the start paddle towards the open goal location. It is possible that individuals that preferentially rotated the start paddle towards the goal

were able to inhibit rotating the start paddle until they had attended to the goal location. There is some evidence to suggest that orangutans outperform other great ape species in other physical problem-solving tasks requiring inhibitory control (Vlamings et al. 2010; Albiach-Serrano et al. 2012), whereas other studies have reported an absence of interspecific differences (Vlamings et al. 2006; Uher and Call 2008).

Inhibition of inappropriate actions may be important for efficient locomotion through the forest canopy (an idea that is touched upon by Vlamings et al. 2010). A large bodied ape moving through the discontinuous, compliant forest canopy is faced with a vast amount of information to process, and must make correct decisions regarding which supports to use and which to avoid, as a wrong choice could result in a fall, causing serious injury, or even death (Thorpe et al. 2009). In this situation, the ability to attend to what lies ahead and mentally 'try out' different actions prior to choosing which route to take would be highly beneficial (Povinelli and Cant 1995; Barth et al. 2004). Others have related apparent differences in inhibitory control skills in primates to differences in their social systems. Specifically, good inhibitory skills have been linked to species with high levels of fission-fusion dynamics (Amici et al. 2008), because of the need to assess a situation before acting, and respond in a way that is appropriate based on the current composition of the party (Aureli et al. 2008). While both orangutans and bonobos are considered to experience high levels of fission-fusion dynamics (Amici et al. 2008), orangutans have a more extended, less cohesive social system (Aureli et al. 2008). This means that intraspecific competition for food, which may promote impulsive food-grabbing behavior, is relatively reduced in orangutans (Shumaker et al. 2001).

Three orangutans but no bonobos solved some of the 2-step trials in experiment 1 by pre-positioning relevant non-food paddles. Orangutans rotated more non-food paddles than bonobos overall, but they were not necessarily relevant. It is possible that this finding may be related to species differences in exploratory behavior and temperament (bonobos have been shown to be shyer of novel things than orangutans; Herrmann et al. 2011),

rather than a difference in cognitive ability.

Why did apes fail in the advance planning task?

Negative results in tests of cognitive ability are notoriously difficult to interpret, because there could be several different causes of failure (Seed et al. 2012). Although experiment 2 removed inhibitory demands, it also eliminated the need to encode how diagonally positioned non-food paddles influenced the path of the reward, so it is difficult to determine the relative contributions of these factors to failure in experiment 1. One way to try and illuminate causes of failure in tasks designed to investigate a particular cognitive ability is to minimise peripheral demands that are simultaneously taxed during testing (Seed et al. 2012). For example, in the case of inhibitory control, it has been demonstrated that replacing food with tokens in the reversed contingency task enables subjects to inhibit the strong behavioural predisposition to select the larger quantity (Boysen and Berntson 1995; Boysen et al. 1996; Kralik et al. 2002; Albiach-Serrano et al. 2007; Addessi and Rossi 2011).

Another way of potentially reducing the inhibitory demands of the task presented in experiment 1 would be to enforce a delay between subjects seeing the paddle-box with the reward present and allowing them to respond. Children are known to be more likely to avoid making an inappropriate prepotent response when a delay as short as two seconds is enforced by the experimenter in several different tests of inhibitory control, and it has been proposed that this is because the delay permits time for passive fading of the prepotent response, rather than allowing time for active computation (Simpson et al. 2012). It would be interesting to see if young children, whose inhibitory control skills are known to show marked improvement between the ages of 3 and 5 years (Carlson and Moses 2001) also struggled with the advance planning task before this age, and whether taking measures to reduce inhibitory demands (e.g. by replacing rewards with tokens or enforcing a delay) might improve their performance.

Having found that orangutans and bonobos fail to perform appropriate actions in advance of acting on a food reward in the advance planning paddle-box task, of particular interest is the affect that inhibition may have on performance. To investigate this further and to better understand the cognitive demands of the paddle-box task, in the next chapter (chapter 4) 4- to 10-year-old children are tested with the paddle-box and measures are taken to reduce the inhibitory demands of the task. The development of performance in both sequential planning and advance planning tasks is also examined.

Chapter 4

DEVELOPMENT OF PLANNING IN 4-TO-10-YEAR-OLD CHILDREN: REDUCING INHIBITORY DEMANDS DOES NOT IMPROVE PERFORMANCE

This chapter, largely in its current form, is under review as:

Tecwyn, E.C., Thorpe, S.K.S., Chappell, J. (2013) Development of planning in 4- to 10-year-old children: reducing inhibitory demands does not improve performance. *Journal of Experimental Child Psychology*

Abstract

There are currently relatively few tasks suitable for testing planned problem-solving in children. We presented 4- to 10-year-old children (n=172) with two planning tasks (sequential planning and advance planning) using the paddle-box apparatus, which was originally designed to investigate the planning skills of non-human apes. First, we were interested in the development of children's performance in the two tasks, and whether the strategies children used to succeed differed between age groups. Performance improved significantly across age groups in both tasks. Strategies for success in the advance planning task differed among age groups, with 4- to 5-year-olds performing more excess actions, and a greater proportion of irrelevant excess actions, than older children. Findings are discussed in relation to the development of performance in tower tasks, which are a commonly used test of planning ability in humans. Second, based on previous findings with apes, we predicted that introducing measures to reduce the inhibitory demands of the advance planning task would improve children's performance. Therefore, in this study we introduced two methodological alterations that have been shown to improve children's performance in other tasks with inhibitory demands: (1) imposing a short delay before a child is allowed to act; and (2) replacing reward items with tokens. Surprisingly, neither of these measures improved the performance of children in any of the age groups, suggesting that contrary to our prediction, inhibitory control may not be a key performance-limiting factor in the advance planning paddle-box task.

4.1 Introduction

Planned behaviour involves considering different sequences of action alternatives and choosing between them prior to acting (McCormack and Atance 2011). It is a complex cognitive process, the development of which occurs in conjunction with and is supported by various key executive function processes. Executive functions are a group of skills necessary for the control of thought and action required for reasoning, planning and problem-solving (Anderson 1998; Baughman and Cooper 2007). Key executive functions include inhibitory control, working memory and task switching (Asato et al. 2006; Baughman and Cooper 2007; McCormack and Atance 2011). Given that there are currently few appropriate tasks for investigating planned problem-solving in young children (McCormack and Atance 2011), this study used a novel paradigm originally designed for testing non-human apes (hereafter apes) to present two planning tasks to children, and explored whether inhibitory control might be a key performance-limiting factor.

Development of planned problem-solving

Tower tasks, such as the Tower of London (ToL; Shallice 1982), are the most commonly used tests of planning ability in humans (McCormack and Atance 2011). In this task participants are presented with two sets of three pegs (start and goal), each with three different coloured discs arranged on each set. The aim of each trial is to rearrange the discs on the start pegs so that they match the configuration of discs on the goal pegs. Problem complexity can be manipulated by increasing the number of moves required to solve the trial, as well as by altering structural features of the problem, such as the number of intermediate moves a participant is required to make (Kaller et al. 2011). The planning demands of the task stem from the need to anticipate the consequences of one's next actions (McCormack and Atance 2011). Efficient performance involves mental representation of the path from the start- to the goal-state, followed by behavioural reproduction of the action sequence (Albert and Steinberg 2011).

Several studies have examined the development of ToL performance across different age groups. Luciana and Nelson (1998) found that 4-year-old children performed poorly in 3-step ToL trials compared with 2-step trials. However, subsequent work by Kaller and colleagues (2008; 2011) demonstrated the significant impact that structural details of seemingly comparable ToL trials (rather than just the number of steps) can have on performance. Kaller et al. (2008) demonstrated that while 4-year-olds were able to solve 3-step trials that did not require an intermediate move (i.e. placing a disc on to a non-goal peg), they struggled when an intermediate move formed part of the solution, despite being instructed to plan their moves before starting. Kaller and colleagues (2008) suggested that the key difference between these two types of 3-step trial was that whereas trials without intermediate moves could be solved using a step-by-step perceptually-guided strategy, those requiring an intermediate more necessitated planning in terms of searching ahead, to anticipate the consequences of at least the first two steps. The authors suggested that development of performance may have been related to a switch in strategy, from a perceptually-guided one to planning ahead (Kaller et al. 2008). Asato et al. (2006) investigated the development of performance in 2- to 5-step ToL problems in 8- to 30-year-olds. Age effects were only found for the more complex 4- and 5-step problems. As age increased, the number of excess moves being made decreased (Asato et al. 2006). Finally, in a study of 10- to 30-year-olds, Albert and Steinberg (2011) found that performance in 3-step ToL trials was not mature until 16- to 17-years of age.

Children under five years find it particularly difficult to follow task instructions in tower tasks (Baughman and Cooper 2007) or to operate commonly used computerised interfaces, such as those used for maze navigation planning tasks (Miyata et al. 2009). There is therefore a need to develop tasks that could be used to test the planning abilities of young children and infants. Furthermore there is a lack of tasks that could potentially be used for cross-species comparisons, which is important if we want to understand something about the evolution of multi-step problem-solving and begin to elucidate which, if any,

underlying cognitive mechanisms humans share with other animals.

The paddle-box paradigm

Tecwyn et al. (2013) developed a novel paradigm (the paddle-box) to investigate the planning abilities of apes. The paddle-box consists of a transparent Perspex box containing eight rotatable paddles on three levels. At the bottom of the paddle-box are four possible goal locations that can each be configured as either open or blocked. Captive orangutans and bonobos were presented with two different tasks: sequential planning and advance planning. In both tasks, the aim of each trial was to turn a number of paddles to move a food reward from its starting position on one of the paddles inside the apparatus (the start paddle) to the open goal at the bottom. The reward could be successfully retrieved in a minimum of one, two or three paddle rotations (classified as 1-, 2- or 3-step trials). The key difference between the tasks was that for 2- and 3-step trials in the sequential planning task subjects could always rotate the start paddle immediately and still potentially succeed. In the advance planning task on the other hand subjects had to pre-position one or two other paddles before rotating the start paddle, because if the start paddle was rotated immediately the reward would become trapped. Both ape species performed well in the sequential planning task, but generally failed in the advance planning task, because they did not pre-position the relevant paddles before turning the start paddle (Tecwyn et al., 2013). The authors suggested that the apes' poor performance in the advance planning paddle-box task may have been due to their difficulty inhibiting the prepotent response to turn the paddle with the highly salient food reward on immediately (and hence failing to perform the appropriate response of pre-positioning the paddles necessary for success; Tecwyn et al., 2013).

A role for inhibitory control in planning tasks?

It is often the case that a task designed to test for a particular cognitive ability (e.g. planning) simultaneously taxes other mechanisms (Seed et al. 2012). Inhibitory control is

one such mechanism and is the ability to stop an inappropriate prepotent response, or to ignore irrelevant information (Simpson and Riggs 2007). An example of a prepotent response is reaching directly for a desirable object (Diamond 1990). Responses may be prepotent because they are biologically predisposed; they are afforded by particular objects; they are habitual; or they are associated with desirable consequences (Simpson and Riggs 2007). Inhibitory abilities develop slowly and are not fully mature until early adulthood (Diamond 2002).

There is evidence that inhibitory control affects performance in tower tasks. Although the ToL does not establish a strong prepotent response that needs to be inhibited in terms of a salient reward item (unlike in the paddle-box task), participants need to inhibit making tempting 'trap' moves (e.g. placing a disc in its goal position when an intermediate move is required), and delay immediate, impulsive responding in favour of planning (Albert and Steinberg 2011). In Kaller et al.'s (2008) study, 4-year-old children's difficulty in solving 3-step trials requiring an intermediate move may have been related to their inability to inhibit making an impulsive but inappropriate first step of placing a disc onto its goal peg. Asato et al. (2006) found that increased success in 4- and 5-step ToL trials was significantly associated with fewer errors in an eye-movement test of response inhibition in 8- to 13-year-olds, and attributed this to the continuing development of voluntary cognitive control into adolescence. In their study of ToL performance in 10- to 30-year-olds, Albert and Steinberg (2011) found that impulse control was the best predictor of performance.

Reducing the inhibitory demands of tasks: delays and tokens

Certain methodological alterations have been shown to reduce the inhibitory demands of tasks and hence improve performance. In this study we test the effectiveness of two particular measures that it is possible to implement with the paddle-box apparatus: imposing a short delay before permitting a child to respond, and replacing rewards with symbolic tokens.

A well-known test of inhibitory control is the 'day-night' task (Gerstadt et al. 1994), in which children are required to say "day" to a picture of a moon, and "night" to a picture of a sun. Three- to-4-year-old children perform poorly, because they struggle to inhibit saying what the stimuli really represent (Gerstadt et al. 1994). Diamond et al. (2002) found that implementing a delay before children were allowed to respond – during which the experimenter sang a short rhyme– enabled 3- to 4-year-olds to succeed. 'Go/no-go' tasks (Livesey and Morgan 1991) have also been employed to investigate the development of inhibitory control in children. In this paradigm children are presented with a series of boxes and told that boxes with a particular cue on the lid contain a reward and should be opened ('go' trials) whereas boxes with a different cue on the lid are empty and should be left shut ('no-go' trials). While 3- to 4-year-old children succeed in opening boxes on go trials, they also frequently incorrectly open boxes on no-go trials, even when instructions are made explicit and there are negative consequences of doing so (Simpson and Riggs 2007). In a version of the go/no-go task, Simpson et al. (2012) found that introducing a 2 second delay between presenting the box and placing the cue on the lid significantly improved children's performance in no-go trials. The authors argued that increasing the time between presentation of the triggering stimulus (the box) and allowing a child to respond permits passive dissipation of the prepotent response to open the box, enabling formation of an appropriate response strategy (Simpson et al. 2012). Mitchell and Poston (2001) compared the performance of two groups of adults in a set of 5- and 6-step ToL trials, all of which required inhibition of one 'tempting' but inappropriate move. Participants in the experimental group were told to stop and think about certain moves whereas participants in the control group were not. Inducing this delay significantly improved performance in terms of the number of trials completed in the minimum number of steps (Mitchell and Poston 2001).

The 'windows' task (Russell et al. 1991) has similar behavioural inhibition demands to the go/no-go task. Here, each child plays with an opponent and is presented with two

boxes with transparent lids: one containing a visible reward and one that is empty. The child is told to point to the box they want their opponent to get, and that they will get to open the other box themselves. Three-year-old children typically and repeatedly fail this task (they point at the box containing the reward and therefore lose it to their opponent), whereas 4-year-olds succeed. Hala and Russell (2001) have suggested that 3-year-olds' difficulty in this task is related to having to inhibit the prepotent response of pointing at the desirable reward, while holding the rules of the task in mind. Apperly and Carroll (2009) found that replacing the reward (stickers) in the windows task with any one of five types of symbol (token), including equally desirable sweets, and a photograph of stickers, significantly improved the performance of 3- to 4-year-olds. The authors concluded that because the children's decision-making is dominated by the desire to obtain the reward, symbols enable them to avoid impulsive responding and think more flexibly, permitting an alternative appropriate response to be formulated (Apperly and Carroll 2009).

The aims of this study were twofold. First, we wanted to examine whether the paddle-box paradigm would detect age differences in performance in the sequential planning task and/or advance planning task (in terms of both success and strategy used), and interpret our findings in the context of the existing literature on the development of performance in tower tasks, given that they are well-established tests of planning ability. If results are comparable, then this would suggest that the paddle-box is an appropriate paradigm for investigating the development of planning in children. We predicted that even the youngest children (4- to 5-year-olds) would perform well in the sequential planning paddle-box task, given that orangutans and bonobos were capable of success (Tecwyn et al., 2013) and 4-year-olds succeed in simple 3-step ToL trials (Kaller et al. 2008). We expected performance in the advance planning task (particularly in 2- and 3-step trials) to improve with increasing age, but possibly not reach ceiling, given that planning ability continues to develop into adolescence (Asato et al. 2006), and 3-step ToL performance may not be mature until 16-17 years of age (Albert and Steinberg 2011).

Second, we investigated whether inhibitory control was a key factor limiting 4- to 10-year-old children's performance in the advance planning paddle-box task, by introducing two methodological alterations that have been shown to improve performance in other tasks with inhibitory demands: implementing a short delay before children were allowed to respond (delay condition), and replacing stickers with symbolic tokens (tokens condition). We predicted that, if inhibitory control was key to successful performance in the advance planning task (because the prepotent desire to rotate the start paddle immediately needs to be inhibited), then more children would succeed in the delay and tokens conditions (where inhibitory demands are reduced), compared with in a control condition. Specifically, we proposed that fewer children should rotate the start paddle immediately and instead succeed in prepositioning relevant paddles in the experimental conditions. We predicted that the experimental conditions should have no effect on performance in the sequential planning task, because in this task children could always rotate the start paddle straight away and still potentially succeed.

4.2 Materials and methods

4.2.1 Participants

The final sample consisted of 172 children: 60 4- to-5-year olds (30 boys and 30 girls, mean age = 5 years 0 months [5;0], range = 4;6 - 5;6), 60 6- to-7-year-olds (31 boys and 29 girls, mean age = 7;1, range = 6;7 - 7;6), and 52 9- to-10-year-olds (26 boys and 26 girls, mean age = 10;0, range = 9;7 - 10;6) from three primary schools in the Birmingham, UK area.

4.2.2 Apparatus: the paddle-box

The paddle-box apparatus was used (Tecwyn et al., 2013), which was originally designed to investigate the planning abilities of apes. For a full description of the apparatus see chapter 3 of this thesis (section 3.2.2 and Fig. 3.1 on page 61). In the present study stickers were used as rewards instead of food items.

4.2.3 Procedure

Children were tested in a quiet area close to their classroom. The experiment was presented as a game where stickers could be won. Children sat at a table with the paddle-box and two experimenters. The main experimenter ran the experiment and coded the data and the second experimenter assisted with configuring the apparatus between trials. Children were alternately assigned to one of three conditions: control, delay or tokens. First, children completed the warm-up exercise to ensure they were able to operate the simple paddle mechanism and retrieve the item from an open goal. All children were then presented with six trials of two different planning tasks: sequential planning and advance planning (12 trials in total). The order in which the two tasks were presented to a child was counterbalanced. Within each task, children were presented with the same set of six trials in the same order. Each trial was a unique configuration of the apparatus, with the minimum number of steps required to retrieve the item (1, 2 or 3), start level and position of the goal location pseudorandomised, with the constraint that none of them was the same for more than two consecutive trials. For each task there were two 1-step, two 2-step and two 3-step trials.

Warm-up task

Children were presented with the apparatus with goals B and C open and A and D blocked (Fig. 3.1a, page 61, chapter 3). They were then given one of two sets of instructions, depending on which condition they were assigned to:

Control and delay conditions: "Every time you manage to get a sticker out of the puzzle you can keep it, OK? You can touch anything on this side of the puzzle (*experimenter indicates front of the paddle-box*). Let's have a practice first"

Tokens condition: "Every time you manage to get a sponge out of the puzzle you will win a sticker, OK? You can touch anything on this side of the puzzle (*experimenter indicates*

front of the paddle-box). Let's have a practice first"

The sticker/sponge was then placed on paddle 7 (bottom centre, see Fig. 3.1a) and the child was asked to try and get it out of the apparatus. If the child failed to do this spontaneously, they were given neutral prompts such as "can you think how you might be able to get the sticker/sponge out?" If they still failed, it was demonstrated to them by the experimenter, and the warm up task was repeated until they spontaneously retrieved the sticker/sponge.

Testing phase

Subjects in all three conditions were given the following instructions: "OK, now that we've had a practice we're going to play the game lots more times so you can try to win some more stickers! I'm going to ask you to cover your eyes and not look each time I set up a new game so it's a surprise - is that OK?"

The next set of instructions varied between conditions as follows:

Control condition: "When I tell you to open your eyes, you can try to get the sticker"

Delay condition: "When I tell you to open your eyes you can look at the puzzle, but please wait until I say 'go' before you try to get the sticker" (*experimenter implements a 2 second delay*)

Tokens condition: "When I tell you to open your eyes, you can try to get the sponge"

Having configured the apparatus, the sticker/sponge was placed on the start paddle by the experimenter. Stickers were oriented so that they were facing the child. If the sticker was retrieved in the control/delay conditions the child peeled the sticker off the sponge and kept it. If the sponge was retrieved in the tokens condition the child passed it to the experimenter in exchange for a sticker. If the item became trapped at one of the blocked

goal locations in any of the conditions it was removed from the back of the apparatus by the experimenter and the child did not receive a sticker for that trial.

Sequential planning task

In the sequential planning task, all of the paddles were set up in a flat orientation at the start of each trial. The number of steps required to solve each trial was dictated by the level at which the reward started. All trials could be solved in a minimum of one, two or three steps. All trials could be solved by rotating the start paddle first, and then by rotating paddles on which the reward was subsequently located (see Fig. 3.2b on page 66 in chapter 3 for an example of how to solve a 2-step sequential planning trial).

Advance planning task

In each trial only the start paddle was positioned in a flat orientation. All of the other paddles were positioned in one of two possible diagonal orientations. This meant that if the start paddle was rotated first, the reward would slide down to the bottom of the apparatus and end up at one of the blocked goal locations. Therefore, the key difference between this and the sequential planning task was that here, in 2- and 3-step trials, children had to pre-position one or two other paddles before rotating the start paddle (see Fig. 3.2a on page 66 in chapter 3 of this thesis for an example of how to solve a 2-step advance planning trial).

4.2.4 Data scoring and analysis

Data were scored live. For each trial, we recorded whether the reward/token was successfully retrieved from the open goal or became trapped at one of the blocked goal locations. The measure of overall performance was the number of correct trials out of six in each task. To examine performance differences between trial-types (1-, 2- and 3-step) the dependent measure was the percentage of children succeeding in at least one out of two trials of that

type. To gain a better understanding of why children might be failing in the advance planning task, the number of children that only rotated the start paddle in every one of their trials was also recorded. Strategies used in the advance planning task were examined by scoring the number of excess paddle rotations performed, together with whether each of these paddle rotations was relevant or irrelevant for retrieving the sticker/token. Relevant paddles were defined as those that could affect the path between the start paddle and the open goal, whereas irrelevant paddles could not.

Data were analysed using IBM SPSS Statistics 21. Non-parametric tests were used and all statistical tests were two-tailed. The significance level of alpha was 0.05.

4.3 Results

Two key questions were investigated. First, we were interested in whether the paddle-box paradigm would detect age-related trends in performance in the sequential planning and/or advance planning task. Specifically, we examined whether older children succeeded in more trials than younger children in both tasks, and whether strategies used to succeed in the advance planning task changed across age groups. Second, we examined whether inhibitory control might be a key performance-limiting factor in the advance planning task, by implementing two methodological alterations that have been demonstrated to improve children's performance in other tasks with inhibitory demands, and analysing their effect on performance measures.

4.3.1 Age-related trends in performance

Number of trials correct

There was no difference in overall performance (number of trials correct) based on gender in either of the tasks (Mann-Whitney U test: sequential planning task: U=3361.0, n=172, p=0.287; advance planning task: U=3134.5, n=172, p=0.079), so data for both genders

were combined for all subsequent analyses.

Within each age group, children succeeded in significantly more trials in the sequential planning task than in the advance planning task (Table 4.1; Mann-Whitney U Test: 4- to 5-year-olds: U=577.0, n=120, $p<0.001$; 6- to 7-year-olds: U=1199.5, n=120, $p=0.001$; 9- to 10-year-olds: U=767.0, n=104, $p<0.001$).

Table 4.1 – Performance by age group for the two tasks

	4 - 5 years	**6 - 7 years**	**9 - 10 years**
Overall trials correct (12)	5.76 ± 0.29	7.57 ± 0.36	9.60 ± 0.24
Sequential planning			
Trials correct (6)	3.85 ± 0.17	4.38 ± 0.21	5.37 ± 0.12
% >1 x 1-step	88.0	90.0	100.0
% >1 x 2-step	85.0	93.3	100.0
% >1 x 3-step	81.7	88.3	100.0
Advance planning			
Trials correct (6)	1.92 ± 0.21	3.18 ± 0.26	4.23 ± 0.22
% >1 x 1-step	86.7	96.7	100.0
% >1 x 2-step	26.7	50.0	76.9
% >1 x 3-step	20.0	50.0	84.6
% start paddle only	65.0	43.3	13.5

Note: '% >1' variables represent the percentage of children succeeding in at least one out of two 1-, 2- and 3-step trials. Numbers in brackets are the total number of trials presented. Values given are percentages or means plus/minus one standard error

The order in which the two tasks were presented had a significant impact on performance in the sequential planning task for all age groups, with children getting significantly more trials correct when the sequential planning task was presented after the advance planning task (Mann-Whitney U Test: 4- to 5-year-olds: U=614.5, n=60, $p=0.012$; 6- to 7-year-olds: U=738.5, n=60, $p<0.001$; 9- to 10-year-olds: U=548.0, n=52, $p<0.001$). In the advance planning task, performance was better when this task was presented second in 6- to 7-year-olds (U=265.5, n=60, $p=0.005$) and 9- to 10-year-olds (U=151.0, n=52, $p<0.001$) but order of task presentation did not affect the performance of 4- to 5-year-olds in the advance planning task (U=340.0, n=60, $p=0.09$).

Sequential planning task: 1-, 2- and 3-step trials

Nine- to 10-year-olds were significantly more likely to succeed in at least one 1-step trial than both 4- to 5-year-olds (Fisher's exact test: p=0.014) and 6- to 7-year-olds (Fisher's exact test: p=0.029; Table 4.1). The performance of 4- to 5-year-olds and 6- to 7-year-olds did not differ. 9- to 10-year-olds were also more likely to succeed in 2-step trials than 4- to 5-year olds (Fisher's exact test: p=0.03) but not 6- to 7-year-olds. The performance of 4- to 5-year-olds and 6- to 7-year-olds did not differ. In 3-step trials, 9- to 10-year-olds were more successful than 4- to 5-year-olds ($\chi^2{}_1$=10.57, n=112, p=0.011) and 6- to 7-year-olds ($\chi^2{}_1$=6.47, n=112, p=0.03). The performance of 4- to 5-year-olds and 6- to 7-year-olds did not differ.

Within each age group, there were no significant differences in success rate between trials requiring a minimum of 1-, 2- or 3-steps (Table 4.1; p>0.05 for all).

Advance planning task: 1-, 2- and 3-step trials

Four- to 5-year-olds were significantly outperformed by 6- to 7-year-olds ($\chi^2{}_1$=3.927, n=120, p=0.048) and 9- to 10-year-olds (Fisher's exact test: p=0.007) in 1-step trials (Table 4.1). The performance of 6- to 7-year-olds and 9- to 10-year-olds did not differ. There were significant differences between the performance of adjacent age groups in both 2- and 3-step trials, with 9- to 10-year-olds more likely to succeed than 6- to 7-year-olds (2-step: $\chi^2{}_1$=8.62, n=112, p=0.003; 3-step: $\chi^2{}_1$=14.89, n=112, p<0.001), and 6- to 7-year-olds being significantly more successful that 4- to 5-year-olds (2 step: $\chi^2{}_1$=11.08, n=120, p=0.001; 3-step: $\chi^2{}_1$=11.87, n=120, p=0.001; Table 4.1).

Within each age group, performance was significantly better in 1-step trials compared with 2-step trials (4- to 5-year-olds: $\chi^2{}_1$=43.982, p<0.001; 6- to 7-year-olds: $\chi^2{}_1$=33.41, p<0.001; 9- to 10-year-olds: $\chi^2{}_1$=13.57, p<0.001), and in 1-step trials compared with 3-step trials (4- to 5-year-olds: $\chi^2{}_1$=53.57, p<0.001; 6- to 7-year-olds: $\chi^2{}_1$=33.41, p<0.001;

9- to 10-year-olds: Fisher's exact test, p=0.006; Table 4.1). There was no significant difference in performance between the 2- and 3-step trials for any of the age groups (Chi square tests, p>0.05 for all).

The overall percentage of children only rotating the start paddle in all advance planning trials (i.e. never pre-positioning any paddles) differed significantly between age groups (Table 4.1). 65.0% of 4- to 5-year-olds only ever turned the start paddle, compared with 43.3% of 6- to 7-year-olds (Chi square test: $\chi^2{}_1$=5.67, n=120, p=0.017). There was also a significant difference between the 6- to 7-year-olds (43.3%) and 9- to 10-year-olds (13.5%; $\chi^2{}_1$=11.96, n=112, p=0.001).

Strategies for success in the advance planning task

Age group had a significant effect on how many excess actions (paddle rotations) were performed in successful 2- and 3-step advance planning trials (Kruskal-Wallis test: $\chi^2{}_2$ =15.09, n=252, p=0.001). Post-hoc pair-wise comparisons revealed that 4- to-5-year-olds were significantly more likely to perform more excess actions in successful trials (4.24±0.49) than 6- to-7-year-olds (2.14±0.20; U=1025.0, n=129, p=0.002) and 9- to-10-year-olds (2.20±0.14; U=1167.0, n=152, p<0.001). The number of excess actions did not differ between 6- to-7-year-olds and 9- to-10-year-olds (U=4441.0, n=219, p=0.303).

Of the excess actions performed by children in successful 2- and 3-step trials in the advance planning task, the percentage that were relevant to solving the task differed as a function of age group (Fig. 5.1).

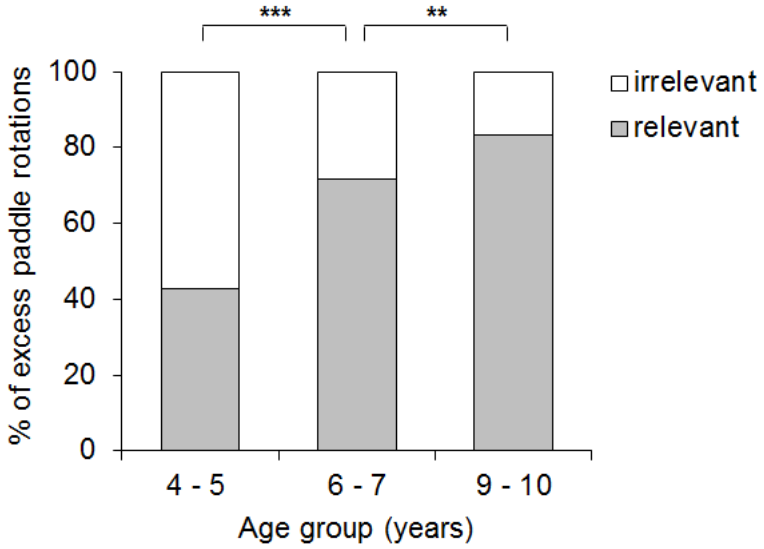

Figure 4.1 – Percentage of relevant and irrelevant excess actions in successful 2- and 3-step advance planning trials as a function of age group. ** indicates $p<0.01$, *** indicates $p<0.001$ in a Chi square test

Only 42.9% of 4- to 5-year-olds' excess paddle rotations were relevant to solving the trial, compared with 71.8% for 6- to 7-year-olds (Chi square test: $\chi^2{}_1=37.77$, n=450, $p<0.001$; Fig. 5.1). There was also a significant difference between the percentage of relevant paddle rotations made by 6- to 7-year-olds (71.8%) and 9- to 10-year-olds (83.3%; $\chi^2{}_1=9.98$, n=524, $p=0.002$; Fig. 5.1).

4.3.2 Is inhibitory control a key performance-limiting factor? Impact of experimental conditions on performance

Experimental condition (control, delay, tokens) did not have a significant effect on the number of trials correct in any of the age groups, in either the sequential planning task (Fig. 4.2a; Kruskal-Wallis test: 4- to 5-year-olds: $\chi^2{}_2=1.74$, n=60, $p=0.419$; 6- to 7-year-olds: $\chi^2{}_2=2.81$, n=60, $p=0.245$; 9- to 10-year-olds: $\chi^2{}_2=0.073$, n=52, $p=0.964$) or the advance planning task (Fig. 4.2b; Kruskal-Wallis test: 4- to 5-year-olds: $\chi^2{}_2=1.05$, n=60, $p=0.591$; 6- to 7-year-olds: $\chi^2{}_2=1.23$, n=60, $p=0.540$; 9- to 10-year-olds: $\chi^2{}_2=0.17$, n=52, $p=0.921$).

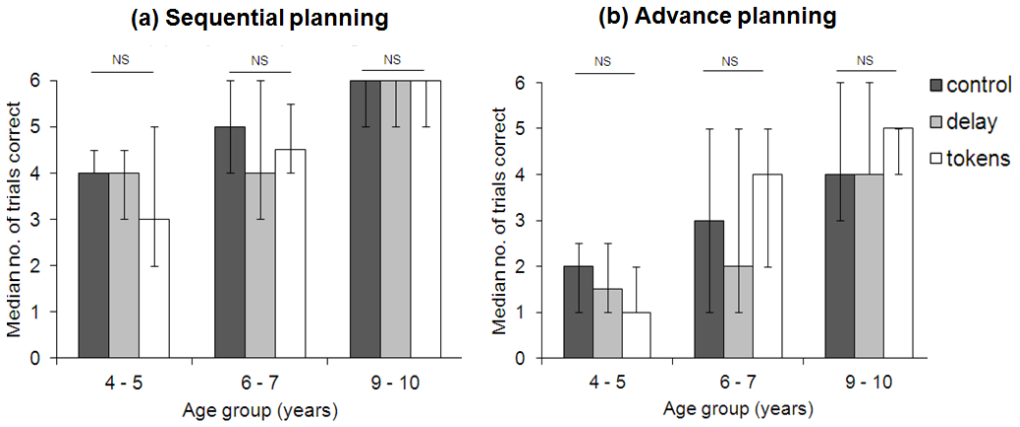

Figure 4.2 – Median number of trials correct for each age group as a function of experimental condition (control, delay, tokens) in (a) the sequential planning task and (b) the advance planning task. Error bars denote the inter-quartile range. NS indicates $p>0.05$ in a Kruskal-Wallis test

The percentage of children only rotating the start paddle did not differ significantly between conditions, within any of the age groups (Fig. 4.3; Chi square test: 4- to 5-year-olds: χ^2_2 =0.44, n=60, p=0.803; 6- to 7-year-olds: χ^2_2 =0.950, n=60, p=0.622; 9- to 10-year-olds: χ^2_2 =0.152, n=52, p=0.927).

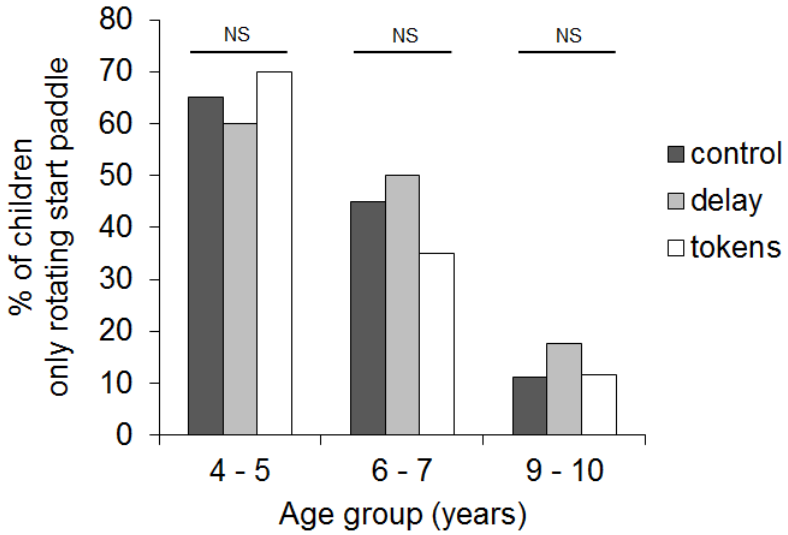

Figure 4.3 – Percentage of children in each age group only rotating the start paddle in all six advance planning trials, as a function of experimental condition. NS indicates $p>0.05$ in a Chi square test

4.4 Discussion

Our primary aims were (1) to investigate the development of performance in the two paddle-box tasks across the three age groups tested, and hence assess its suitability for a test of planning in children given that few appropriate tasks currently exist; and (2) to better characterize the cognitive demands of the paradigm by establishing whether inhibitory control was a key factor limiting children's performance in the advance planning task.

Development of planned problem-solving: age-related trends in paddle-box performance

Children in all age groups performed significantly better in the sequential planning task than in the advance planning task. This is as expected, given the relative complexity of the two tasks. This finding also reflects the results of a previous study with apes (Tecwyn et al. 2013). The two tasks share some key demands, including the need to locate the item to be retrieved (start paddle), locate the open goal, and work out an appropriate sequence of paddle rotations to get the item from start paddle to the goal. There are however some key differences. The sequential planning task is visuospatially simpler as all of the paddles are flat, so the item can be controlled in a step-by-step manner. Therefore, it is possible to use a perceptually-guided strategy (turn the paddle with the item on towards the open goal) that incrementally moves the item towards the goal. This is true of 3-step ToL trials without any intermediate moves, which 4- to 5-year-olds are able to solve (Kaller et al. 2008). In the advance planning task, relevant paddles need to be pre-positioned before the start paddle is rotated, which requires the anticipation of one's actions, and planning in terms of searching ahead. This task can be likened to ToL trials with intermediate moves, which 4- to 5-year-olds struggle to solve (Kaller et al. 2008).

In both tasks, the average number of trials correct increased across age groups. In the

sequential planning task all age groups performed well in all trial types (1-, 2- and 3-step). Even in the 3-step trials, 81.7% of 4- to 5-year-olds succeeded in at least one out of two trials. Children within a given age group performed equally well across all trial-types; i.e. there was no evidence that they found 3-step trials more difficult than 1-step trials in the sequential planning task. This may be because it was possible to solve all of these trials using a perceptually-guided strategy, which Kaller and colleagues (2008) suggested 4-year-olds were capable of using to solve ToL trials.

There was more variation in performance in the advance planning task across age groups, particularly in the 2- and 3-step trials. Only 20.0% of children in the youngest age group succeeded in at least one 3-step trial, compared with 84.6% of 9- to 10-year-olds. In both 2- and 3-step trials, success increased across the age groups. Unlike in the sequential planning task there was also variation between different trial-types within each age group. Specifically, for all age groups, performance was significantly worse in 2- and 3-step trials compared with 1-step trials. This suggests that younger children found it difficult to look ahead and realise that other paddles had to be rotated before turning the start paddle, as is thought to be the case for ToL trials with intermediate moves (Kaller et al. 2008). To gain a better understanding of why children were failing in the advance planning task, we examined the number of participants that only rotated the start paddle in every one of their trials (i.e. during the task they never rotated any paddles apart from the start paddle). The percentage of children doing this decreased significantly with age, possibly due to the ongoing development of voluntary cognitive control (Asato et al. 2006). Furthermore, unlike older children, 4- to 5-year-olds performed badly in the advance planning task regardless of the order in which the two tasks were presented. It is possible that the youngest children had difficulty 'thinking outside the box' of the most obvious option (i.e. turning the paddle with the item on) (Apperly and Carroll 2009), whereas the older children were better able to overcome this having had some (albeit limited) experience with the apparatus.

Age-related trends in performance: strategies for success in the advance planning task

Because the advance planning paddle-box task can be solved in a variety of ways, it enables the examination of different strategies for success. Four- to 5-year-olds performed significantly more excess paddle rotations when solving 2- and 3-step advance planning trials than children in the two older age groups. Asato et al. (2006) similarly found that excess moves decreased with increasing age in 4- and 5-step ToL trials. These findings reflect the fact that children in the youngest age group frequently solved 2- and 3-step advance planning trials by immediately setting up all of the paddles in a flat configuration, and then retrieving the item in a step-by-step manner as in the sequential planning task (Tecwyn, personal observation). Older children on the other hand were more likely to pre-position paddles diagonally, and therefore take fewer moves to solve a trial. These strategies clearly differ in the amount of planning required to achieve them, but are nevertheless equally effective. Of the excess actions performed in successful trials, older children were more likely to perform excess actions that were relevant to solving the task, as opposed to moving irrelevant paddles (i.e. paddles that could not influence the path between the item and the goal). This likely reflects older children's better understanding of the task, and greater efficiency in problem-solving, possibly afforded by greater allocation of cognitive resources to planning, or a switch to a strategy of planning ahead rather than one based on the use of perceptual cues (Kaller et al. 2008).

At present there is a lack of appropriate tasks for testing the planning skills of young children and infants (McCormack and Atance 2011). The paddle-box provides a paradigm that may be more suitable than the currently available alternatives. Because the paddle-box was originally designed for use with apes, it has the benefit of not requiring the subject to understand complex verbal instructions or adhere to specific rules, unlike in the ToL where participants have to understand, for example, that they are only allowed to move one disc at a time.

Comparison with ape performance

Direct comparisons of the performance of different species using identical tasks are essential if we are to understand what distinguishes one species from one another in terms of cognitive abilities (Dunbar et al. 2005). It is possible to draw some comparisons between the findings of the current study and Tecwyn et al.'s (2013) findings with apes using the paddle-box, but caution is always required when making cross-species comparisons (Boesch 2007). There are inevitably unavoidable differences in testing, including number of subjects, number of trials, time frame of testing, testing environment, conspecific experimenter and verbal instructions for children, morphological differences and reward type. However, designing tasks like the paddle-box that are operated via simple motor actions (turning paddles) and allow children and apes to interact with the apparatus in the same way (using their morphologically similar hands) maximizes the validity of comparisons. Hopper et al. (2010) increased the validity of child-ape comparisons in their study by presenting children with the test apparatus inside a transparent box with access holes, thus mimicking the physical barrier between apes and the apparatus that is formed by the mesh of their enclosure.

The apes in Tecwyn et al.'s (2013) study performed most comparably with the 4- to 5-year-old children in this study. Both groups succeeded in the sequential planning task, regardless of the minimum number of steps required to retrieve the item. Apes and 4- to 5-year-olds struggled in the advance planning task, and in most trials only rotated the start paddle (i.e. failed to pre-position any paddles). Also, unlike the two older age groups of children, apes and 4- to 5-year-olds rotated a high proportion of irrelevant paddles.

Is inhibitory control a key performance-limiting factor? Impact of experimental conditions on performance

Neither of the two methodological alterations that were introduced to reduce the inhibitory demands of the advance planning task (imposing a short delay and replacing stickers

with tokens) improved the performance of children in any of the age groups. Specifically, the experimental conditions did not reduce the likelihood of children performing the inappropriate response of always turning the start paddle immediately, which we suggested was the prepotent response that needed to be inhibited to enable success in the advance planning task (Tecwyn et al., 2013). This is surprising given that both of these measures have been demonstrated to reduce the likelihood of inappropriate prepotent responses in other tasks (Mitchell and Poston 2001; Apperly and Carroll 2009; Simpson et al. 2012). Although the non-inhibitory demands of paddle-box are different from those of the go/no-go task, windows task and ToL, the inhibitory demands of all four tasks stem from the requirement for behavioural inhibition of a prepotent manual response, as opposed to cognitive interference due to competing equivalent verbal responses, as is the case in the day-night task.

It therefore seems that inhibition of prepotent responding was not sufficient to enable success in the advance planning task. Albert and Steinberg (2011) found that prepotent response inhibition was not a predictor of ToL performance in 10- to 30-year-olds. The authors argued that as well as inhibiting immediate responding, participants also needed to sustain this delay in order to engage in effortful planning, and the development of this impulse control was reflected in the maturation of performance in complex ToL trials (Albert and Steinberg; 2011). However, whereas the ToL does not prime a strong prepotent response, the paddle-box does due to the salience of the desirable sticker. Therefore, the inhibitory demands of the advance planning task in this study are arguably higher than those in the ToL.

Other measures may have improved children's performance, such as instructing them to plan their actions before starting or telling them to retrieve the item in the fewest possible moves (both of which improve ToL performance in adults: Phillips et al. 2001; Unterrainer et al. 2003). It is however questionable whether the youngest children in this study would have understood and followed such instructions, and we wanted to maintain potential for

comparability with non-human studies, and therefore chose measures that could potentially be implemented in studies with other species. Delays have been implemented in non-human studies of problem-solving, for example by presenting the test apparatus behind a transparent Perspex barrier so that all of the components were visible but could not be manipulated, and then removing the barrier after the delay period (e.g. Miyata et al. 2011). Tokens have also successfully been used in place of rewards in several studies with non-human primates (e.g. Evans et al. 2012).

Conclusions

This study has demonstrated that the paddle-box is an appropriate tool for investigating the development of planning ability in children, thereby providing a paradigm that is more suitable for comparative investigations of planned problem-solving skills in children and non-human primates than the currently available alternatives. There were clear developmental trends in performance, particularly in the advance planning task. Results from the sequential planning task suggest that, in keeping with other studies (e.g. Kaller et al. 2008; Miyata et al. 2009), the ability to plan a simple sequence of actions is present in early childhood, particularly where it is possible to succeed using a perceptually-guided strategy. The capacity to plan a sequence with intermediate actions that requires looking ahead, as was required for success in the advance planning task, increases throughout childhood and is not mature by 10 years of age. Contrary to our predictions, inhibition of a prepotent response was not found to be a key performance-limiting factor for children in the advance planning task, based on the methodological alterations that were implemented in this study. It is possible that it is not inhibition in terms of simply avoiding an inappropriate response that limits performance in the advance planning task, but young children's (and apes') limitations in allocating sufficient cognitive resources to planning an appropriate response (Asato et al. 2006), or difficulty 'thinking outside the box' of the most obvious option.

Given that ceiling performance was not observed in 9- to 10-year old children in the advance planning task, the performance of adults is examined in the next chapter (chapter 5). Also of interest is whether adults, like apes and children, also perform excess paddle rotations, and/or rotate paddles that are irrelevant to solving trials.

Chapter 5

HOW DO ADULT HUMANS PERFORM IN THE ADVANCE PLANNING PADDLE-BOX TASK?

Abstract

In the field of animal cognition, assumptions are frequently made regarding how adult humans would perform in tasks designed for testing the cognitive skills of animals. In this study adult humans (n=32) were tested in the advance planning paddle-box task, which was originally developed to investigate the planning abilities of non-human apes. Adults did not perform 'perfectly', with over a quarter of participants failing in at least one trial. Most participants made several excess moves when solving trials and some even moved parts of the apparatus that were irrelevant to solving the task. Irrelevant actions were performed less frequently when participants were given 5 seconds to complete a trial, compared with when their time was unrestricted. Verbal explanations by participants suggested that they moved irrelevant parts of the apparatus to increase the 'safety' of the task and 'make sure' the item did not become trapped. Results are discussed in relation to previous findings on the performance of apes and children in the advance planning task. This study and the findings of others demonstrate that adults do not necessarily perform as expected in physical cognition tasks. This highlights the importance of testing adult in cognitive tasks designed for animals, to provide a context in which to interpret the performance of animals and to avoid making assumptions about how humans would perform.

5.1 Introduction

Novel tasks are frequently developed to investigate the cognitive abilities of non-human animals (hereafter animals). However, when testing animals and reporting results of their performance, implicit assumptions are made regarding how adult humans would solve the same problems (Silva et al. 2005). For example, it is frequently assumed that when solving physical problems adults would make use of the causal knowledge that they are known to possess (Silva et al. 2005), such as an understanding of gravity or connectedness, rather than using arbitrary perceptual cues such as colour or continuity. In fact, we rarely know how adults faced with problems designed to test animals would respond (Anderson 2001).

Using adult humans as test subjects enables us to examine decision-making in physical problem-solving tasks, whilst being confident that behaviour is not being influenced by factors that are known to influence the behaviour of animals, such as species-specific predispositions, a lack of cognitive ability, or too great a cognitive load (though these factors may indeed vary between human individuals; Silva and Silva 2010). It also helps to provide a context in which to interpret the performance of animals in similar tasks (Silva and Silva 2012). Furthermore, if and when humans do perform in an unexpected way, we have a luxury that is not available to animal cognition researchers: we can ask them to explain their actions rather than having to draw inferences from their behavioural responses, which may assist with the interpretation of decision-making in non-verbal animals (Silva et al. 2005; Silva and Silva 2010; 2012). It should however be noted that there are issues with subjective reports about higher mental processes, such as the fact that information may be missing or erroneous, and some authors have questioned the validity of findings based on people's post-hoc verbal explanations of their problem-solving behaviour (e.g. Nisbett and Wilson 1977).

Several studies by Silva and colleagues (2005; 2006; 2008; 2010; 2012) have aimed to

increase our knowledge of human adult performance in some of the key tasks designed to test the physical cognition skills of animals; including the trap-tube, trap-table, string-pulling and tool selection tasks. The trap-tube (Visalberghi and Limongelli 1994) is a clear plastic tube with a trap at its centre. A reward is placed at one side of the trap, and in order to retrieve it a stick tool must be inserted at the end of the tube farthest away from the reward, to push it away from the trap and out of the opposite end of the tube. If the tool is inserted at the end of the tube closest to the reward, the reward will be pushed into the trap. Capuchins (*Cebus apella*) and chimpanzees (*Pan troglodytes*) have struggled to solve this task, even across dozens of trials (Visalberghi and Limongelli 1994; Limongelli et al. 1995; Povinelli 2000). In a 'critical condition' designed to investigate what a chimpanzee that had previously succeeded in the original version of the trap tube problem understood about the task, Reaux and Povinelli (2000) presented a version of the trap-tube with the trap inverted, so that it was positioned at the top of the tube, rendering it ineffective. When the previously successful chimpanzee continued to insert the tool at the end of the tube farthest from the reward (in 39/40 trials), the authors concluded that the subject lacked any causal understanding of the relation between the tool, reward and trap; rather she was using a perceptual rule based on the position of the trap (Reaux and Povinelli 2000). This interpretation is problematic, first because there is no incentive for subjects to alter their behaviour just because the trap is ineffective (Chappell 2006), and second because Reaux and Povinelli (2000) implicitly assumed that humans would revert to random responding when presented with the same task. Silva et al. (2005) investigated this, and found that in fact, contrary to the assumption of random responding, in 52/60 trials adults exhibited the same bias as Reaux and Povinelli's (2000) chimpanzee: they inserted the tool at the end of the tube farthest from the reward, despite the absence of an effective trap. Such findings with adults have helped to identify conceptual problems in cognitive tasks (Silva et al. 2005), and the trap-tube paradigm has been subsequently developed and refined in order to minimise the methodological concerns previously associated with it (e.g. Mulcahy and Call 2006b; Seed et al. 2006; Tebbich

et al. 2007; Seed et al. 2009b). This has enabled more valid conclusions regarding animals' causal understanding to be drawn.

Another related test of physical cognition that has been frequently presented to animals is the trap table (Povinelli and Reaux 2000). In this task there are two rakes, each with a reward positioned in front of them (i.e. between the head of the rake and the test subject). One of the rakes also has a functional trap in front of it, whereas the other rake has a painted square, or non-functional 'trap' in front of it, which shares surface-level perceptual features with the genuine trap. To solve this task the subject should pull the rake behind the painted 'trap', and hence avoid the reward falling in to the functional trap. Overall, Povinelli and Reaux's (2000) chimpanzees did not exhibit a preference for pulling the rake on the side of the painted 'trap'. Comparable studies with capuchins and gibbons (*Bunopithecus hoolock*) have produced similar findings, though some subjects may have solved the problem through learning associative rules (Fujita et al. 2003; Cunningham et al. 2006). In a study by Santos and colleagues (2006) tamarins (*Saguinus oedipus*) also failed in the trap table task, however vervet monkeys (*Cercopithecus aethiops*) successfully avoided the functional trap at above chance level (65% of trials).

Silva and colleagues (2005) presented adults with a schematic version (a drawing, rather than the actual apparatus) of the trap-table task. However, the configuration between the rakes, rewards and traps was such that either rake could be selected and the reward would not fall in the trap. Surprisingly, subjects exhibited a strong bias to select the rake on the side of the painted 'trap'. When questioned about their decision-making, they all indicated that they felt the reward was less likely to be lost if they selected the rake on the side of the painted 'trap' (Silva et al. 2005). Further investigation using a real version of the task produced comparable results to the schematic version, and revealed that several variables aside from the presence of a real trap controlled people's behaviour; including the distance between a trap and the reward and the distance over which the reward had to be raked to be retrieved (Silva and Silva 2006). Therefore, as was the case with the inverted trap-tube,

findings with adult humans suggest that an absence of random responding should not be taken to indicate a lack of understanding of the causal features of the task.

Further studies have revealed that in string-pulling tasks, where physical connection between the string and an object is key to success, humans can also be influenced by amount of contact (Silva et al. 2008) and perceptual continuity (Taylor et al. 2012). In a stick-tool selection task, humans consistently selected a tool that was longer than required to retrieve an item from a tube (Silva and Silva 2010), whereas New Caledonian crows (*Corvus moneduloides*) tended to select tools of a length that matched the distance over which a reward had to be retrieved (Chappell and Kacelnik 2002).

Taken together, these findings demonstrate that human adult performance in a variety of physical cognition tasks cannot be assumed, and that relatively small methodological and procedural alterations in task presentation may significantly alter behaviour, which has important implications for the study of physical cognition in other animals (Silva and Silva 2010).

Tecwyn et al. (2013) developed a novel paradigm (the paddle-box) to investigate the planning abilities of non-human apes (hereafter apes) in a physical problem-solving context. The paddle-box consists of a transparent Perspex box containing eight rotatable paddles on three levels. At the bottom of the paddle-box are four possible goal locations that can each be configured as either open or blocked. The aim of each trial is to turn a number of paddles to move a food reward from its starting position on one of the paddles inside the apparatus (the start paddle) to the open goal at the bottom. The reward can be successfully retrieved in a minimum of one, two or three paddle rotations (classified as 1-, 2- or 3-step trials). In the advance planning task subjects have to pre-position one or two other paddles before rotating the start paddle. Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) performed poorly in this task, because they failed to pre-position relevant paddles before turning the start paddle (Tecwyn et al. 2013). Four- to five-year-old

children also struggled to solve the task, and ceiling performance was not observed in 9- to 10-year-olds (Tecwyn et al. under review).

Having tested apes with the paddle-box (Tecwyn et al. 2013), and given the often surprising performance of adults in other tests of cognitive ability designed for testing animals, the main aim of this study was to investigate the performance of adults in the advance planning paddle-box task. We were particularly interested, given previous findings with apes (Tecwyn et al. 2013) and 4- to 10-year-old children (Tecwyn et al. under review) in whether adults would solve trials in the minimum number of steps or whether they would perform excess paddle rotations. We were also interested in whether adults, like apes and children, would rotate paddles that were irrelevant to solving trials. Finally, we investigated whether constraining the time people had to complete the task might result in performance differences, compared with people who had unrestricted time to complete the task. For example, it is possible that when put under time pressure people might spend less time preparing and act more impulsively, potentially making more errors and exhibiting behaviours that caused apes and some children to fail in the task. Alternatively, limiting time for preparation may cause adults to solve the task more efficiently (i.e. perform fewer actions) than when time is unconstrained.

5.2 Materials and Methods

5.2.1 Participants

A total of 32 unpaid participants (20 female, 12 male) with ages ranging from 18 to 41 years (mean: 21 years and 9 months) took part in this study.

5.2.2 Materials

The paddle-box apparatus was used, which was originally developed to investigate the planning abilities of apes (Tecwyn et al. 2013). For a full description of the apparatus see

chapter 3 of this thesis (section 3.2.2 and Fig. 3.1 on page 61). The item to be retrieved from the apparatus was a cube-shaped piece of sponge measuring approximatley 2 cm x 2 cm x 2 cm.

5.2.3 Procedure

Each participant was tested individually and pseudorandomly assigned to one of two conditions: control (n=16) or 5-second (n=16), with the constraint that males and females were equally distributed between the two conditions.

The same twelve advance planning trials were presented to each participant in the same order, with each trial requiring a minimum of between one and three steps (paddle rotations) to retrieve the item. Each trial was a unique configuration of the apparatus, with the minimum number of steps, start level and goal location pseudorandomised, with the constraint that none of them was the same for more than two consecutive trials. For a full description of the advance planning task see chapter 3 of this thesis (section 3.3.2, page 66). There were four 1-step, four 2-step and four 3-step trials. All 12 trials could be solved in a minimum of 24 steps in total.

All participants were shown the paddle-box apparatus and given minimal task instructions; specifically they were not informed of the minimum number of moves in which the item could be retrieved; nor were they instructed to plan their actions prior to starting. Participants were instructed to close their eyes between each trial so that they did not see the next trial being set up. They were then given the following instructions, depending on the experimental condition to which they were assigned:

Control condition: "Your task is to retrieve the item from the paddle-box. You may begin when I tell you to open your eyes"

5-second condition: "Your task is to retrieve the item from the paddle-box. You will

have five seconds from when I tell you to open your eyes"

Pilot work established that it was possible to complete a trial in 5 seconds, but this duration was sufficiently short to put participants under some time pressure. Participants in the 5-second condition had a large timer displayed next to them, which was started by the experimenter when they were told to open their eyes.

5.2.4 Data scoring and analysis

Trials were video recorded for later analysis. For each trial we recorded whether the item was successfully retrieved from the open goal or became trapped at one of the blocked goal locations. The total number of paddle rotations performed was also recorded, together with whether each of these paddle rotations was relevant or irrelevant for retrieving the item. Relevant paddle rotations were defined as those that could affect the path between the start paddle and the open goal, whereas irrelevant paddles could not. Preparation time was recorded using a stopwatch, defined as the time between the participant opening their eyes and performing their first paddle rotation.

Data were analysed using IBM SPSS Statistics 21. Preparation time data were log-transformed to enable parametric statistics to be used. When it was not possible to use parametric statistics because transformation did not result in normally distributed data, non-parametric tests were used. All statistical tests were two-tailed. The significance level of alpha was 0.05.

5.3 Results

5.3.1 Overall performance

The item became trapped in a total of 11/384 trials. These were all 2- or 3-step trials, and the item became trapped because participants failed to preposition all of the relevant paddles before turning the start paddle. Eight subjects (25.0%; two male, six female)

failed to retrieve the item from the goal location in one trial and one subject (female) lost the item in three trials. Of the 11 trials in which the item became trapped, eight were lost by participants in the 5-second condition and three in the control condition. Two participants (both female) retrieved items in some trials (one and three, respectively) by turning the start paddle and then quickly positioning relevant paddles once the item was already moving.

5.3.2 Excess paddle rotations

Only 18.8% of subjects completed all of the trials in the minimum number of steps (24), by prepositioning relevant paddles diagonally and not making any additional paddle rotations. Two subjects performed 21 excess paddle rotations each. The number of paddle-box trials completed in the minimum number of steps did not differ significantly between the control and 5-second conditions (Chi square test: $\chi^2{}_1$=0.227, n=378, p=0.634) and neither did the total number of excess paddle rotations (Mann-Whitney U test: U =17585.5, n=378, p>0.645).

The majority (76.9%) of excess paddle rotations were relevant to solving the trial; however six subjects (18.8%) rotated multiple paddles that were irrelevant to solving the trial (i.e. paddles that could not influence the path between the item and the goal). When questioned about these irrelevant excess actions after completing all the trials, participants consistently responded that they 'wanted to make sure they [the irrelevant paddles] were out of the way'.

Although the total number of excess paddle rotations was similar in the control and 5-second conditions (Fig. 5.1), the ratio of relevant to irrelevant excess paddle rotations differed significantly between conditions (Chi square test: $\chi^2{}_1$=5.535, n=143, p=0.019).

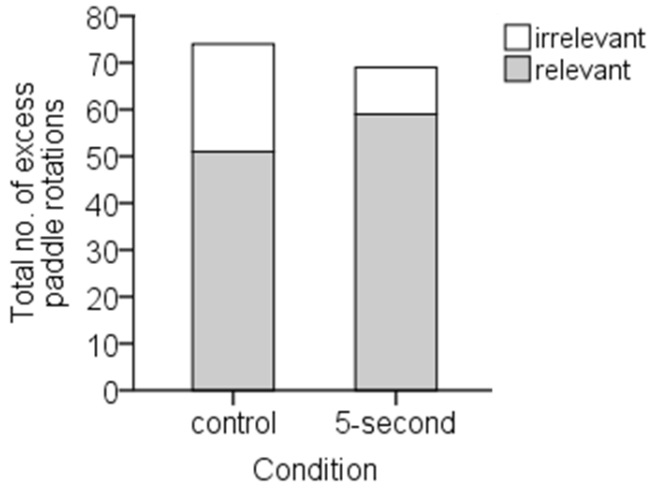

Figure 5.1 – Total number of excess paddle rotations made by all participants in the control and 5-second conditions in the paddle-box task, and the proportion of those paddle rotations that were relevant and irrelevant to retrieving the item

In the control condition 31.1% of excess paddle rotations were irrelevant, compared with 14.5% in the 5-second condition (Fig. 5.1).

5.3.3 Euclidean direction to goal

One of the trials (trial 4) could be solved in a single step, but doing so required rotating the start paddle away from the Euclidean direction to the goal location (Fig. 5.2a).

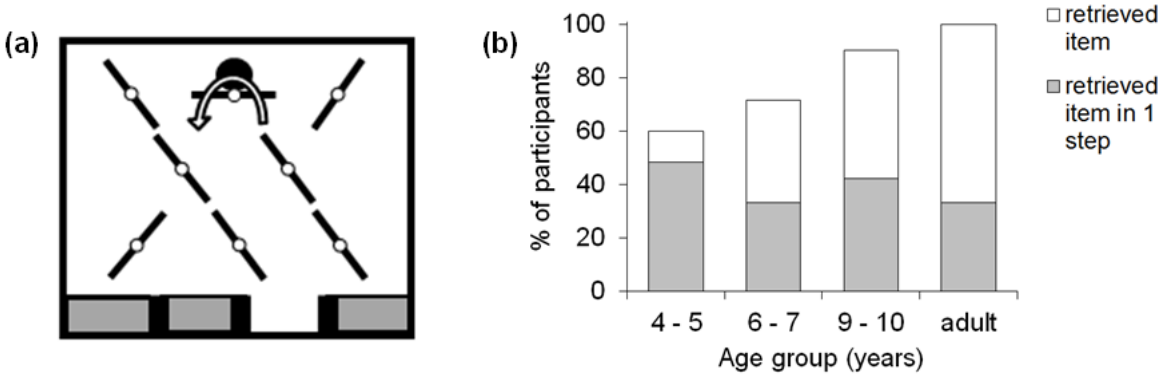

Figure 5.2 – (a) Schematic example of an advance planning paddle-box trial in which the item can be retrieved in 1 step by turning the start paddle away from the Euclidean direction to goal, and (b) a comparison of the performance of 4- to 10-year-old children (Tecwyn et al., unpublished data) and adults in this type of trial

Although all 32 adult participants successfully retrieved the item in this trial, only 11 of

them (four male, seven female) retrieved the item in a single paddle rotation (Fig. 5.2b). In contrast, although only 60.0% of 4- to 5-year-olds succeeded in a comparable trial, the majority of those children (80.6%) did so in one step (Fig. 5.2b). Approximately half of 6- to 7- and 9- to 10-year-olds that succeeded did so in a single paddle rotation (Fig. 5.2b). One out of five orangutans and two out of three bonobos that completed a trial comparable to trial four is this study retrieved the reward item in a single step (Tecwyn et al., unpublished data). All other ape subjects lost the reward because they turned the start paddle towards the goal location, which resulted in it becoming trapped.

5.3.4 Preparation time

Log preparation time for each trial was entered into an ANOVA with condition, gender and minimum number of steps (1-step, 2-step or 3-step) as between-trial factors. All three factors had a significant effect on trial preparation time (condition: $F_{(1,368)}$=108.452, p<0.001; gender: $F_{(1,368)}$=21.942, p<0.001; minimum number of steps: $F_{(2,368)}$=6.470, p=0.002). There were no significant interactions between any of the factors.

Post-hoc t-tests revealed that average trial preparation time was significantly shorter in the 5-second condition compared with the control condition (Fig. 5.3a) and males had a significantly shorter average trial preparation time than females (Fig. 5.3b).

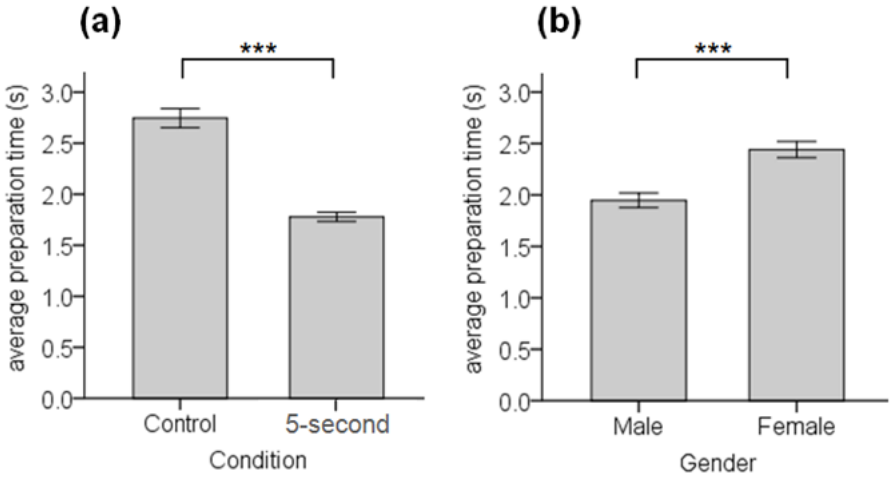

Figure 5.3 – Factors influencing average (mean ± 1 S.E.) trial preparation time: (a) condition; (b) gender; *** indicates p<0.001 in a post-hoc t-test

Post-hoc t-tests with Bonferroni correction revealed that average trial preparation time was significantly shorter in 2-step trials compared with 3-step trials (Fig. 5.4d). There was no significant difference in preparation time between 1- and 3-step trials (p=1.000) or 1- and 2-step trials (p=0.053), though preparation times tended to be longer in 1-step trials compared with 2-step trials (Fig. 5.4d).

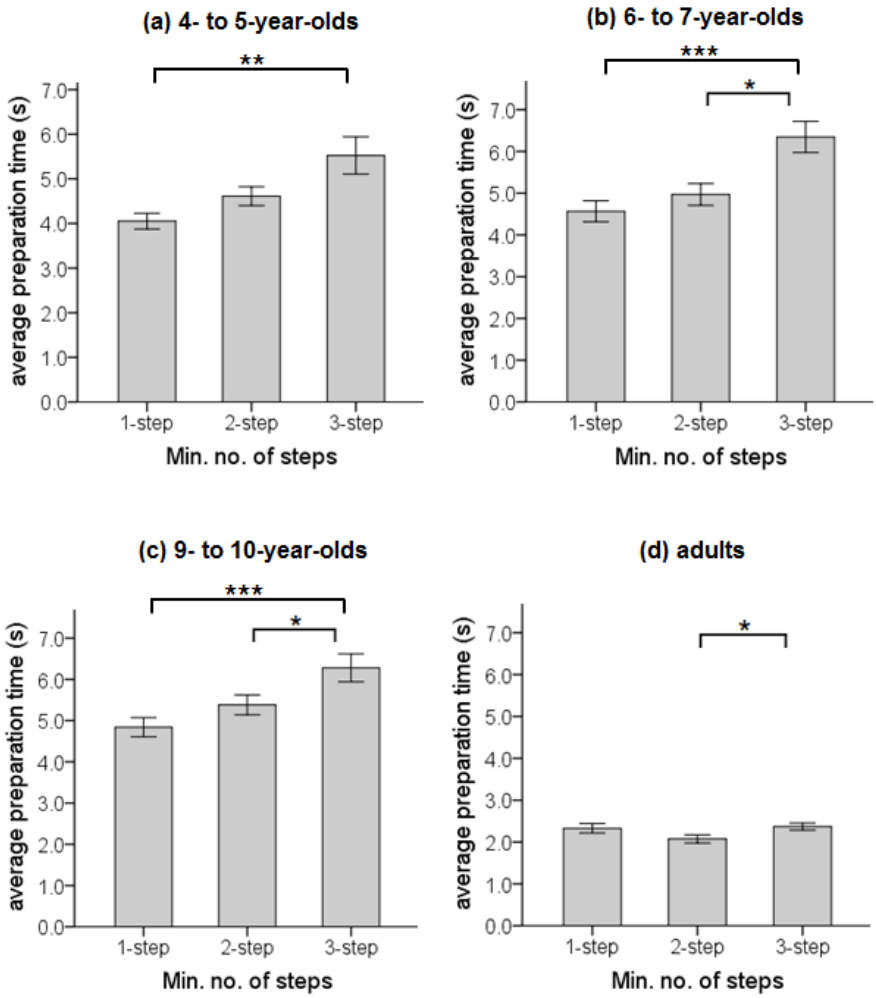

Figure 5.4 – Influence of the minimum number of steps required to solve a trial on average preparation time in (a) 4- to 5-year-olds; (b) 6- to 7-year-olds; (c) 9- to 10-year-olds (Tecwyn et al., unpublished data); and (d) adults. * indicates p<0.05, *** indicates p<0.001 in a post-hoc t-test with Bonferroni correction

Analysis of variance also revealed a significant main effect of minimum number of steps on average log preparation time for children within each of three age groups tested in the advance planning task (Tecwyn et al., unpublished data). Post hoc t-tests with a

Bonferroni correction revealed that for 4- to 5-year-olds there was a significant difference in preparation time between 1- and 3-step trials only (p=0.002; Fig. 5.4a). For the 6- to 7-year-olds and 9- to 10-year-olds there was a significant difference in preparation time between 1- and 3-step trials (p<0.001 for both) and 2-step and 3-step trials (p=0.014 and p=0.046, respectively; Fig. 5.4b and 5.4c).

5.4 Discussion

This study examined the performance of adult humans in the advance planning paddle-box task. The results demonstrate that adults don't perform 'perfectly', or necessarily as expected, which is in keeping with findings from other studies in which adults have been tested with cognitive tasks originally designed for investigating the abilities of animals (Silva et al. 2005; 2008; Silva and Silva 2006; 2010; 2012; Taylor et al. 2012). This study also showed that in the paddle-box task, adults sometimes perform irrelevant actions, as do apes and children. Also, rather than causing adults to make more errors, constraining the time available to them to complete the task increased their problem-solving efficiency in terms of reducing the number of irrelevant paddles that they rotated.

Although adult humans were predictably more successful than apes in the advance planning paddle-box task, over a quarter of participants failed to retrieve the item from the open goal location in at least one of their 12 trials because they did not preposition all of the relevant paddles before turning the start paddle, suggesting that the task is non-trivial for adults. Eight out of 11 items were lost in the 5-second condition, but the sample was too small to establish whether the experimental condition influenced the likelihood of this occurring. Two subjects retrieved the item in some trials by positioning paddles after they had turned the start paddle, demonstrating that it is possible to succeed in the advance planning task without making a complete plan and executing the planned action sequence before turning the start paddle.

The majority of participants performed some excess paddle rotations that were not necessary for retrieving the item. This mainly occurred when participants solved 2- and 3-step trials by setting up the paddles involved in the path between the item and goal in a flat configuration, rather than prepositioning them diagonally. They then moved the item down through the levels in a step-by-step manner, thereby rotating each of the relevant paddles twice instead of the minimum of once. Despite being less efficient in terms of number of actions, such a strategy enables greater control over the item, and therefore may potentially be perceived as 'safer'. Some 4- to 10-year-old children also used this strategy, but only when they had previously solved a task in which all of the paddles started in a flat configuration (sequential planning task; Tecwyn et al. under review).

Perhaps surprisingly, despite average preparation time being significantly shorter in the 5-second condition compared with the control condition, the total number of excess paddle rotations, and the number of trials solved in the minimum number of moves did not differ between conditions. Phillips et al. (2001) also found no difference in the number of excess moves or trials solved in the minimum number of moves in the Tower of London (ToL) task when people were either instructed to fully pre-plan their response, or given only 5 seconds to plan. The authors suggested that people may in fact carry out online planning from scratch during execution of the task, regardless of how long they have spent pre-planning (Phillips et al. 2001). However, as online planning is difficult in the advance planning paddle-box task, given that once the start paddle has been rotated it is not easy to change the path of the item, it seems more likely that in the present study a lack of difference in these performance measures between conditions is due to all of the trials being fairly easy for adults.

When the apes in Tecwyn et al.'s (2013) study rotated paddles that were irrelevant to solving a trial, it was interpreted as a probable lack of knowledge of the way in which the paddles could influence the path of the reward. However, in this study six adults also rotated a number of irrelevant paddles, and this occurred significantly less often in

the 5-second condition than in the control condition. Taken together with their verbal explanations of wanting to make sure those paddles were 'out of the way' it seems that, given unlimited time to solve a problem, some adults may be cautious in their approach, performing additional actions to increase 'safety' and the perceived likelihood of success. However, when time is limited, less time is allocated to preparation, so they are less cautious and more efficient in their physical problem-solving.

Adults' behaviour in trial four of this study is of interest, particularly when considered together with the behaviour of children and apes in a comparable trial, as it reveals differences in problem-solving strategy. The majority (21/32) of adults chose to make excess moves in trial four, which enabled them to turn the start paddle towards the goal, rather than make a single move that required turning away from the goal. This suggests that most participants were strongly influenced by the Euclidean direction to the goal, which may again be related to what they perceived to be the 'safer' strategy. Children who succeeded in this type of trial were more likely to do so in a single step (Tecwyn et al. unpublished data), possibly because they behaved less cautiously than adults. Euclidean direction to goal has been shown to influence the decision making of capuchin monkeys (*Cebus apella*) in 2D maze navigation, with subjects particularly likely to make errors when the correct route required moving away from the Euclidean direction to the goal (Fragaszy et al. 2003; 2009). Orangutans in Tecwyn et al.'s (2013) study also preferentially rotated the start paddle towards the goal location in the advance planning paddle-box task. In the present study, seven females and four males solved the trial in a single step (by turning the start paddle away from the Euclidean direction to goal). It would be interesting to see if a larger sample size would reveal a gender difference in how this trial was solved by adults, given that males are, for example, more likely to use Euclidean strategies when giving directions, whereas females are more likely to use landmarks (Dabbs et al. 1998).

Males had significantly shorter preparation times than females, though this should be interpreted with caution due to the small sample size. Speculatively, this could be related

to gender differences in visuospatial abilities (e.g. Vecchi and Girelli 1998). Males may find it easier to visualise the path from the item to the goal, and hence require less preparation time than females. Alternatively, it may be that spending longer on preparation before tacking a problem may be a choice reflecting personality characteristics such as impulsivity (Phillips et al. 2001).

Interestingly, adult preparation time did not relate to the minimum number of steps required to solve a trial in the way we might have expected. When 4- to 10-year-old children were tested in a comparable set of advance planning trials, average preparation time increased in a step-wise manner with increasing minimum steps; that is average preparation time was significantly longer in 3-step trials compared with 1-step trials within each age group tested (Tecwyn et al., unpublished data). This is in keeping with findings from ToL studies where preparation time increases with increasing minimum number of moves (Luciana et al. 2009; Albert and Steinberg 2011). However, for the adults tested in this study preparation time was longer in 3-step trials than 2-step trials, but 1-step trials had a significantly longer average preparation time than 2-step trials, and did not differ from 3-step trials. This may reflect the fact that all of the trials presented in this study were relatively straightforward for adults, as indicated by their shorter preparation times compared with children. Also, unlike in ToL where all 1-step trials are equally simple, 1-step advance planning paddle-box trials vary in their complexity. In their most simple form the item to be retrieved starts on the bottom level of the paddle-box, and the participant simply has to turn the paddle towards the goal directly beneath. However, the item could also start on the top level, so that the item and goal are separated by a greater distance than in the former example, and retrieving the item might require the paddle to be turned away from the Euclidean direction to goal (as in trial four). It is reasonable to expect that the latter trial type might require more consideration, and hence longer preparation time, than the former type. This likely resulted in an increased average preparation time for adults in 1-step trials overall.

This study and the findings of others show that adult humans often do not perform as we might expect in 'simple' tasks designed to probe various cognitive abilities of animals. In the advance planning paddle-box task adult humans, like apes, sometimes failed to retrieve the item; performed excess actions, some of which were irrelevant to solving the task (particularly when time was unrestricted); and seemed to be influenced by Euclidean direction to goal. Therefore, when developing novel tests of cognitive skills, animal cognition researchers should strive to test adult humans in as comparable a way as possible, to provide a context in which to interpret their findings with animals and to avoid making assumptions about how humans would perform.

Having developed a task appropriate for comparative investigation of planned problem-solving (chapters 3, 4 and 5), attention is next turned to another aspect of physical problem-solving that may be particularly relevant to great apes: understanding of object compliance. In chapter 6 orangutans are presented with a puzzle-tube containing vertical barriers that impede the retrieval of a food reward, to investigate whether they use barrier thickness as a visual cue to predict their compliant properties.

Chapter 6

DO CAPTIVE ORANGUTANS (*PONGO PYGMAEUS*) USE DIAMETER AS A VISUAL PREDICTOR OF COMPLIANCE?

Abstract

Moving around on compliant arboreal supports is a key challenge faced by wild orangutans. How do they achieve safe and efficient locomotion, particularly during gap crossing? For natural materials such as branches, diameter is a predictor of compliance. The aim of this study was to investigate whether captive orangutans (*Pongo pygmaeus*) use thickness as a visual predictor of the compliant properties of barriers in a problem-solving context. Three orangutans were presented with the task of retrieving a reward from the centre of a transparent tube. The tube contained two vertical barriers of equal length that had different compliant properties. The barriers partially obstructed the passage of the reward, because the gap beneath each of them was too small for the reward to pass underneath. In each trial, only one of the two barriers was sufficiently compliant to afford passage of the reward underneath it. Three different conditions were presented. In the first condition the barriers were designed to reflect the natural relationship between thickness and compliance; i.e. the thinner barrier was the compliant one. In two further conditions, thickness was decoupled from compliance, so that it could no longer be used as an accurate predictor. Based on the initial direction that subjects chose to move the reward in, there was minimal evidence that orangutans used thickness to predict compliance in this context. One subject frequently explored the barriers haptically, and the information she extracted guided her behaviour. The possibility remains that wild orangutans use diameter as a predictor of arboreal support compliance during locomotion. More ethologically valid experimental paradigms may be more likely to reveal such abilities, should they exist.

6.1 Introduction

Knowledge of the functional properties of objects is key to many animals' success in the physical world. Of interest from a cognitive perspective is how individuals extract relevant information and select appropriate objects when faced with challenges such as extractive foraging, nest building, or arboreal locomotion. Some relationships between the perceptual and functional properties of objects are directly and accurately perceivable based on visual characteristics. Consider for example a stick tool: the stick's length directly relates to whether or not it can be used to obtain an out-of-reach food item, and its diameter determines whether or not it can be inserted into a hole of a given size. There is considerable experimental evidence demonstrating that non-human animals (hereafter animals) are able to select appropriate tools based on directly perceivable properties, including length (Chappell and Kacelnik 2002; Mulcahy et al. 2005; Sabbatini et al. 2012), diameter (Chappell and Kacelnik 2004) and shape (Bird and Emery 2009).

Other relationships between an object's visual appearance and its properties are more complex, as its affordances (action possibilities; Gibson 1977) are based on invisible structural features, or features that only become apparent once some action is taken, rather than perceptually-based exemplars (Penn and Povinelli 2007). Weight and compliance (i.e., flexibility) are examples of such properties, as they both depend on an object's material. For example, two stones of the same size would have different weights if one stone was sandstone and another was granite. Similarly, a living branch and a dead branch of the same length and thickness would have different compliant properties. What mechanisms could be involved in obtaining information about the invisible properties of objects? Do individuals use visual cues to predict an object's invisible functional properties? Are they able to learn about features of objects that are not directly perceivable? Or do they need to experience these properties directly via exploratory manipulation?

Vonk and Povinelli (2006) argue that non-human primates are unable to recruit unob-

servable forces or entities to explain or predict the behaviour of objects. However, some behaviour observed in the wild is indicative of knowledge of unobservable object properties and how they relate to task demands. Chimpanzees select appropriate stones for to use for nut-cracking according to the properties of different nuts (Boesch and Boesch 1983) and use 'tool-sets' comprising sticks with different compliant properties (e.g. rigid sticks for digging and compliant sticks for fishing) for extractive foraging of honey (Brewer and McGrew 1990) and termites (Sanz et al. 2004). In a year-long field study of bearded capuchins (*Cebus libidinosus*), resistance of the food item a subject was attempting to crack open was found to predict the weight of the hammer stone used (Spagnoletti et al. 2011).

It is not only in the context of tool use that apparent knowledge of invisible object properties is found. Living wooden branches and trunks are the most common natural compliant substrates, and they are most frequently encountered by habitually arboreal animals (Channon et al. 2011).The great apes are an arboreal clade and the challenges they face in the physical world are exacerbated by their large body size (Byrne 1997). Being a large bodied animal living in highly compliant, fragile arboreal habitat poses challenges related to safe and effective locomotion and foraging that are not faced by smaller-bodied animals (Cant 1992). An ability to predict the compliant properties of arboreal supports would be highly advantageous given the potentially high cost of trial-and-error learning, and the fact that it is not always possible to directly explore a support's properties (e.g. if it is located on the far side of a gap to be crossed). A recent study by van Casteren et al. (2012) suggested that wild Sumatran orangutans (*Pongo abelii*) selected nest building materials on the basis of their compliant properties. They used more rigid branches for the structural parts of the nest and more compliant branches for the lining, and seemed to select them on the basis of their diameter (van Casteren et al. 2012). It is also known that support diameter is associated with locomotor mode in wild Sumatran orangutans (Thorpe and Crompton 2005), and it has been suggested that the greatest challenge faced by the

last common ancestor of the great apes was safe, efficient locomotion in a fragile, compliant arboreal environment (Povinelli and Cant 1995). Orangutans are able to successfully navigate gaps in the canopy during arboreal locomotion. Gaps to be crossed may appear to be a given size based on current visual information alone, e.g. the distance between two horizontal supports ('visual gap', Figure 6.1a). However, the size of a gap may change dynamically as a result of the compliant properties of the supports and the actions and weight of the animal (e.g. a support might deform downwards creating a larger 'functional gap', Figure 6.1b).

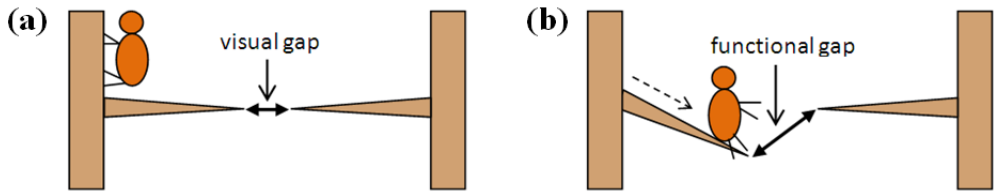

Figure 6.1 – Schematic diagram of a large-bodied arboreal animal approaching a gap between adjacent supports that appears to be of a given size (a: the visual gap); but changes size as a result of support deformation to produce a larger functional gap (b); a product of the animal's mass and the support's compliant properties

In the wild branch diameter is a reliable and easily observable indicator of its compliance (van Casteren et al. 2012, 2013). It therefore seems feasible that orangutans (as the only extant great ape to remain exclusively in the terminal branch niche) might use the diameter of supports as a predictor of their compliant properties during arboreal locomotion, and potentially be able to infer something about how these properties relate to the size of a functional gap to be crossed in the forest canopy.

Although observational evidence for animals selecting objects with appropriate invisible properties is strong, there is a need for controlled experiments to probe the underlying mechanisms involved in such behaviour. Several studies have investigated captive animals' understanding of the compliant properties of tools, with mixed findings. In the flimsy tool problem (Povinelli et al. 2000), subjects must select between two rakes for pulling in an out of reach reward: one with a rigid head and one with a compliant head. Only

the rake with the rigid head can be used to retrieve the reward. Despite direct experience of the tool materials, and demonstration of their properties by the experimenter, six out of seven chimpanzees failed to select the rigid tool for raking more than would be expected by chance (Povinelli et al. 2000). When Kacelnik and colleagues (2006) replicated Povinelli et al.'s (2000) experiment with a captive New Caledonian crow, they found that the subject chose the functional tool with rigid head in 100% of initial trials, but her performance rapidly declined over the course of each testing session (Kacelnik et al. 2006). In contrast, cotton-top tamarins (*Saguinus oedipus*) and vervet monkeys (*Cercopithecus aethiops*) reliably selected a functional rigid tool rather than a nonfunctional flimsy tool across 24 trials (Santos et al. 2006). More recently, chimpanzees, bonobos (*Pan paniscus*), orangutans and capuchins (*Cebus apella*) have all demonstrated the ability to select a tool with appropriate compliant properties for retrieving a reward, from a set of two or three tools (Walkup et al. 2010; Manrique et al. 2010, 2011). They were able to do so whether they experienced the tools' properties themselves, or had the properties demonstrated to them by the experimenter. Subjects were sensitive to the task demands as they were able to select a compliant tool rather than a rigid tool when required, and they were also able to ignore irrelevant perceptual features such as colour (Manrique et al. 2010, 2011).

The aforementioned studies have indeed shed some light on animals' understanding of the compliant properties of tools. Findings suggest that at least some subjects are able to select tools with appropriate compliant properties to meet different task demands. However, none of these studies addressed whether subjects might use visual cues to predict compliance. An elegant study by Visalberghi and colleagues (2009) examined wild capuchins' (*Cebus libidinosus*) use of size as a visual cue for predicting the weight of stones to be used for nut cracking. Eight capuchins were initially presented with a small versus a large stone of the same material, and they reliably touched the large stone first (and subsequently transported it and used it to crack open a nut; Visalberghi et al. 2009). In order to probe this selection process further, Visalberghi and colleagues (2009) also presented the

capuchins with novel artificial stones, the invisible functional properties of which had been manipulated so that they could not be accurately judged based on their visual appearance. For example, in a 'conflicting size and weight' condition, subjects were presented with a large light stone, a small light stone and a small heavy stone. In a further condition, stones of the same size that had different weights were presented. The aim of artificially confounding object properties is to violate the expectations of the test subject, prompting a re-initiation of exploration in order to resolve the discrepancy experienced (Chappell et al. 2012). In all of the artificial stone conditions where visual cues could not be used to accurately predict weight, the capuchins touched the heavier functional stone first less often than in the natural condition. However, they were successful in transporting and using the functional stones because they used exploratory behaviours such as lifting and tapping, from which they could extract relevant information regarding the stones' weight (Visalberghi et al. 2009).

Exploratory behaviour may be particularly important when an object's properties cannot be perceived via vision alone. It is known that humans spontaneously carry out specific exploratory procedures that optimise the uptake of desired information about an object; for example, haptic exploration in the form of application of force by pressing or bending an object is commonly used to extract information about its compliance or hardness (Lederman and Klatzky 1987). Children have been shown to explore object compliance in the context of selecting an appropriate tool for a task (Klatzky et al. 2005) and judging whether a handrail was sufficiently rigid to facilitate crossing a narrow bridge (Berger et al. 2005).

To our knowledge, no study has experimentally tested whether great apes use diameter as a visual cue to predict compliance. As the only great ape to remain in the terminal branch niche, orangutans might be expected to have continued to face strong selection pressures for behaviour that enables safe, efficient arboreal locomotion, compared with the other extant great apes. Therefore, the aims of this study were to investigate the following

questions:

1. Do captive orangutans (*Pongo pygmaeus*) use thickness of a vertical barrier to predict its compliant properties, and to infer how this will affect the size of a functional gap?
2. Do captive orangutans use appropriate exploratory procedures to extract information regarding the barriers' compliant properties?

6.2 Materials and methods

6.2.1 Subjects and housing

Three orangutans housed at Apenheul Primate Park, Netherlands participated in this study (Table 6.1).

Table 6.1 – Study subjects: sex, age in years and whether they were born in captivity (C) or in the wild (W)

Subject	**Sex**	**Age**	Birthplace
Amos	M	9	C
Sandy	F	27	C
Silvia	F	44	W

6.2.2 Apparatus

The apparatus was attached to the outside of the enclosure and consisted of a transparent Perspex puzzle-tube (75 cm x 12 cm x 10 cm) with open ends (the same tube as used in chapter 2 but with the gap and trap elements and end pieces removed so that the base of the tube was continuous). Vertical barriers that varied in thickness and compliance could be inserted into the top of the puzzle-tube. Thick barriers were approximately three times wider than thin barriers. Compliant barriers were made out of rubber and non-compliant barriers were made out of metal or plastic. All barriers had a similar black, matte appearance. In each trial the reward (a walnut) started in the centre of the tube and there was a single vertical barrier at each side of the tube (see Fig. 6.2).

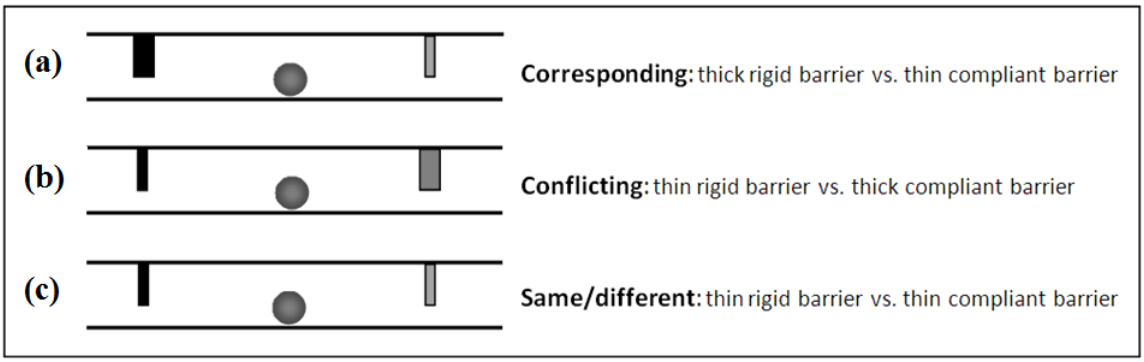

Figure 6.2 – Schematic diagram of test apparatus showing the three different compliant conditions that were presented to subjects. In each trial the reward (grey circle) started in the centre of the tube and there was a single vertical barrier at each end of the tube. In each condition (a-c) black represents the non-compliant barrier and grey represents the compliant barrier (N.B. the barriers used in the apparatus all had a black, matte appearance)

Subjects manipulated the reward through a series of finger holes in the tube. They could also explore the barriers directly through these holes. The vertical barriers were sufficiently long that the 'visual gap' between the bottom of both barriers and the base of the tube was too small for the reward to pass through (1.5 cm). Therefore, in order to access the reward via either end of the tube (which were both open) the subject had to displace a barrier sufficiently to create a larger 'functional gap' (see Fig. 6.3a).

Figure 6.3 – Schematic diagram of a compliant barrier being displaced (a), creating a 'functional gap' large enough for the reward to pass through; and a non-compliant barrier, the affordances of which do not permit passage of the reward (b). Dashed arrows represent the direction in which the reward is being pushed by the subject

In each trial the compliant properties of the two barriers meant that only one of them afforded passage of the reward (see Fig. 6.3), so the reward could only be accessed via one end of the tube (i.e. the side with the compliant barrier). Three different compliant conditions were presented (see Fig. 6.2). In corresponding condition (Fig. 6.2a), subjects

were presented with barriers designed to reflect natural compliant properties, i.e. the thinner barrier was more compliant than the thicker barrier. In the next two conditions subjects were presented with pairs of barriers where compliance did not predict thickness, i.e. the functional properties were decoupled from the visual cue of thickness. In the conflicting condition (Fig. 6.2b), thickness and compliance were confounded so that the thicker barrier was more compliant than the thinner barrier. In the same thickness/different compliance (S/D) condition (Fig. 6.2c), the two barriers were the same thickness, but one was compliant and one rigid.

If subjects used thickness as a visual cue for assessing a barrier's compliant properties then the following performance outcomes would be predicted for the three conditions:

1. **Corresponding**: subjects should move the reward in the direction of the thin barrier (correct) more often than expected by chance
2. **Conflicting**: subjects should again move the reward in the direction of the thin barrier (incorrect) more often than expected by chance
3. **Same thickness/different compliance** (S/D): subjects should perform at chance-level, as barrier thickness cannot be used as a cue

If haptic exploration plays an important role in extracting information regarding objects' unobservable properties, subjects might be expected to use appropriate exploratory procedures (e.g. pushing against the barriers) to determine which barrier is compliant.

6.2.3 Testing procedure

Subjects were tested in separation rooms (10-15 m^2) where they were held on a regular basis for feeding and cleaning purposes. Each condition was presented a total of twenty times, in two blocks of ten trials. Orientation of the compliant barrier (and hence the end from which the reward could be retrieved) was pseudorandomised within each block, with the constraint that the compliant barrier could not appear at the same side of the tube

for more than two consecutive trials. The corresponding condition was presented first, followed by two blocks of each of the other two conditions in a random order. Subjects received no more than one session per day and were tested in isolation except for one adult female (Sandy) who was accompanied by two dependent juveniles. Subjects were not food deprived before the trials, water was available *ad libitum* and they could choose to stop participating at any time. One subject (Silvia) became inattentive during a testing session and refused to return to the apparatus for the next trial despite encouragement. The session was therefore terminated and completed two days later. Otherwise, subjects remained motivated to obtain the rewards (walnuts) throughout the study.

6.2.4 Data scoring and analysis

All trials were videotaped. For each trial the following data were scored:

1. whether the **initial choice of direction** (defined as the direction in which the subject first moved the reward, even if this was subsequently switched) was:
   a) correct (towards the compliant barrier) or incorrect (towards the rigid barrier)
   b) to the left or right
2. **latency (s) to reward retrieval**, defined as the time from a subject's initial contact with the reward to the time when the reward passed under the compliant barrier
3. the **number of deliberate switches of the reward's direction** of movement made by a subject. A deliberate switch was defined as a subject actively changing the direction of the reward's movement, by pushing it from the opposite side to that used previously. If a reward rebounded backwards from a barrier due to the force applied to it by a subject in a forwards direction this did not count as a deliberate switch of direction
4. **latency (s) to an initial deliberate switch of direction**, defined as the time between a subject first contacting one barrier with the reward and the subject making a deliberate change of direction, as defined above

5. occurrences of **haptic exploration of barriers**, defined as any direct physical contact with a barrier, excluding pushing the reward against it

Two-tailed binomial tests were used to assess whether individual subjects' initial choice of direction across the 20 trials for each condition differed from what would be expected by chance (50% correct) and whether they showed any directional biases. Latency data were log-transformed to allow parametric statistical analysis. Where transformation did not result in data appropriate for parametric analyses, nonparametric statistical tests were used. General linear models (GLMs) were used to investigate which factors influenced latency to reward retrieval and latency to an initial switch of direction. Condition, block and whether the initial choice of direction was correct or incorrect were included as fixed factors, and subject was included as a random factor. Where significant effects were found and there were more than two levels within a factor, a series of post-hoc pairwise Tukey tests were performed to find the source and direction of the significance. Alpha was set at 0.05. Due to the infrequency of exploratory behaviour, these data are described qualitatively. Data were analysed using PASW Statistics 18 (IBM SPSS Inc. 2009).

6.3 Results

6.3.1 Initial choice of direction

Table 6.2 shows the number of trials in which subjects chose the correct initial direction (i.e. towards the compliant barrier) for the three different compliant conditions (n=20 for each).

Table 6.2 – Number of trials out of 20 in which the correct initial direction was chosen by each subject in the three different compliant conditions. * indicates $p<0.05$ in a binomial test. Italic values in brackets indicate the number of correct trials (out of 10) in block 1 and block 2, respectively.

Subject	**Compliant condition**		
	Corresponding	Conflicting	Same/different
Amos	9 (*4,5*)	7 (*3,4*)	10 (*5,5*)
Sandy	7 (*2,5*)	5* (*3,2*)	9 (*3,6*)
Silvia	9 (*4,5*)	13 (*7,6*)	7 (*4,3*)

Sandy's performance differed significantly from what would be expected by chance in the conflicting condition (binomial test: 5 out of 20 trials correct; p=0.041; see Table 6.2). No other performances of any of the subjects in any of the compliant conditions differed significantly from 50% of trials correct ($p>0.05$ for all).

Across the whole experiment (60 trials) Sandy exhibited a preference to initially move the reward to the left and Silvia tended to move it to the right (binomial test: $p<0.001$ and p=0.007 respectively). Amos did not exhibit a directional bias in his initial choice of direction (binomial test: p=0.245).

6.3.2 Latency to reward retrieval

Five trials were excluded from the retrieval latency analyses, either because the reward broke part way through the trial (after the initial choice of direction was recorded) and could therefore fit beneath either barrier, or because the subject left the apparatus. Latency to retrieve the reward ranged from 2 to 181 seconds. Condition significantly affected how long it took to retrieve the reward (GLM: $F_{(2,163)}$= 3.86; p=0.02). Post-hoc pairwise comparisons revealed that there was a significant difference between time taken to retrieve the reward in the corresponding condition compared with the same/different condition (p=0.007), but not between any of the other conditions ($p>0.05$ for all). Whether the initial direction in which the reward was moved was correct or incorrect had a significant effect on latency to reward retrieval ($F_{(1,163)}$ = 38.17; $p<0.001$; Fig. 6.4).

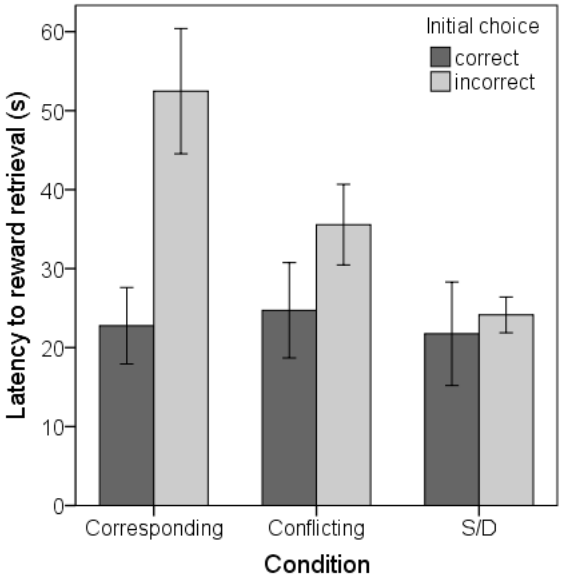

Figure 6.4 – Mean±SE latency to retrieve the reward from the tube in the different compliant conditions, depending on whether the initial choice of direction in which to move the reward was correct or incorrect.

There was also a significant effect of block on latency to reward retrieval ($F_{(1,163)}$=9.24; p=0.003), with latency being longer in the first block compared to the second block (Fig. 6.5a). There were no significant interactions between fixed factors.

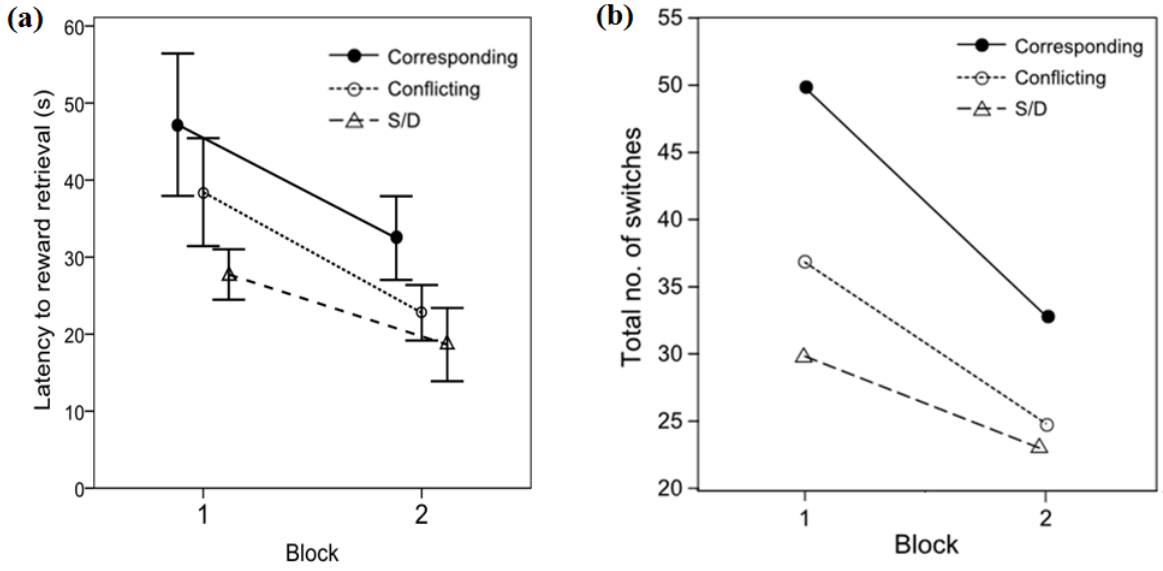

Figure 6.5 – Change across testing blocks for each compliant condition in (a) latency to retrieve the reward (mean ± 1 S.E.); and (b) the total number of deliberate directional switches of the reward. S/D = same thickness/different compliance condition

6.3.3 Directional switches

Directional switches occurred in 64.4% of all trials. In the 102 trials in which the incorrect initial direction was chosen, a directional switch was necessary to retrieve the reward (i.e. to move the reward towards and under the correct, compliant barrier). In 79.8% of these trials, only the single required switch was made. When the correct initial direction was chosen and the compliant barrier that could be displaced sufficiently was contacted, subjects did still sometimes subsequently switch direction and move the reward towards the incorrect barrier (in 19 out of 78 trials).

There was a pattern of fewer directional switches in the second block compared with the first block across all conditions, though this was never significant (Mann-Whitney U tests: $p>0.05$ for all). In both blocks, the most switches occurred in the corresponding condition, followed by the conflicting condition, with the fewest switches occurring in the same thickness/different compliance condition.

6.3.4 Latency to initial switch of direction

The time taken for subjects to deliberately switch the direction of the reward's movement inside the tube following its first contact with one of the barriers ranged from 2 to 47 seconds. Testing block had a significant effect on the latency to the first deliberate switch of direction (GLM: $F_{(1,104)}= 6.51$; $p=0.01$), with more rapid switching occurring in block 2 (Fig. 6.6).

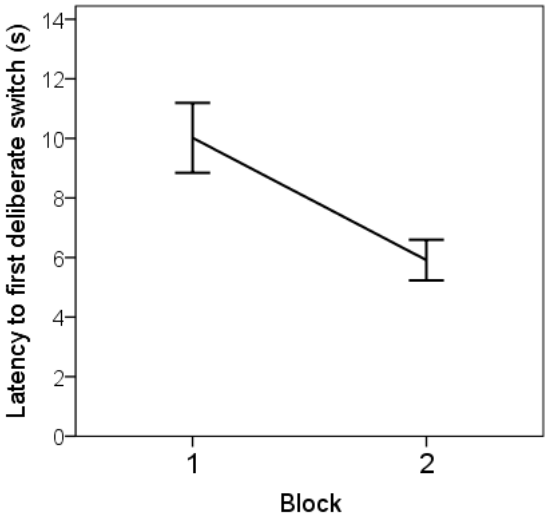

Figure 6.6 – Change across testing blocks in the latency (mean ± 1 S.E.) from the first contact with a barrier to a deliberate switch of reward movement direction

There was no effect of compliant condition or whether the initial choice of direction was correct or incorrect on latency to the first deliberate switch of direction, and there were no significant interactions between any of the factors (p>0.05 for all).

6.3.5 Exploration of barriers

Only one subject (Silvia) regularly explored the barriers haptically, by pushing against them with a single finger. She exhibited this behaviour a total of 32 times, including in her first trial. Twenty-eight of her barrier explorations (87.5%) were of the incorrect (non-compliant) barrier. She explored barriers most frequently (13 times) in the Conflicting condition and all of these explorations involved the incorrect barrier. On five occasions, Silvia was moving the reward towards the incorrect barrier, but before the reward contacted the barrier she explored it with her finger, and subsequently changed the direction in which she was moving the reward. Amos haptically explored a barrier (the correct, compliant one) once, in his second to last trial, before the reward was inserted into the apparatus. He subsequently moved the reward in the direction of this barrier.

6.4 Discussion

The aim of this study was to investigate whether captive orangutans used thickness as a visual cue to predict the compliant properties of barriers impeding the passage of a food reward, and whether they might explore barriers haptically to extract relevant information about their affordances. To do this we presented orangutans with the task of retrieving a reward from a tube containing two vertical barriers that impeded its passage. Subjects did not appear to base their initial choice of direction in which to move a reward on the thickness of the barriers. This suggests that they were not using thickness as a perceptual cue to infer the barriers' compliant properties. Our predictions about which of the two barriers subjects should move the reward towards if solely using thickness as a predictor of compliance were not met, except for in the same thickness/different compliance condition, where random responding was predicted. In fact, subjects' performances did not differ from chance-level (50% of trials correct) across any of the conditions, except for Sandy's performance in the conflicting condition. She only chose the correct initial direction (towards the thicker, compliant barrier) in five out of twenty trials across the two blocks of ten trials, which differed significantly from what would be expected by chance. It is possible that Sandy was using barrier thickness as a visual predictor of compliance, perhaps having learned to associate the thinner barrier with successful reward retrieval in the corresponding condition that was presented first. She may have subsequently transferred this learned rule ('the reward can be accessed via the thinner barrier') to the conflicting condition, where it was no longer appropriate. This seems unlikely however, as she did not perform very well in the corresponding condition (2/10 and 5/10 trials correct in blocks 1 and 2 respectively). Sandy and Silvia showed significant left and right directional preferences respectively over the 60 trials, which may have contributed to their overall chance-level performances.

It is possible that the subjects may have become proficient at using thickness as a cue for predicting compliance in the task if they had been presented with further blocks of trials

and their performance had been allowed to reach asymptote. This was found to be true of capuchins' navigation of 2D mazes in a study by Pan et al. (2011). However, this was not the aim of the current study; of interest here was whether subjects would use thickness as a visual cue for predicting compliant properties from the outset of the problem, not whether they could learn to do so over time by association.

Although it has previously been argued that latency may not be an appropriate measure when comparing performance between different species (chapter 2), it may be informative when trying to understand the decision making processes of individuals of the *same* species when presented with different experimental conditions. On average it took subjects significantly longer to retrieve the reward in the corresponding condition compared with the same thickness/different compliance condition, but it seems likely that this was related to the fact that subjects generally became faster with increasing experience of the apparatus, as indicated by shorter latency to reward retrieval in block 2 compared to block 1 for all conditions. Across all conditions, latency to retrieve the reward was significantly longer when the initial direction of reward movement was incorrect. This seems obvious, but it is worth noting because taking longer to obtain the reward might be considered to be a cost to subjects. Evans et al. (2012) suggested that the 1-2 seconds taken to exchange a token for food may have been long enough to hinder the performance of captive capuchins (*Cebus apella*) in a delayed gratification task. In this study however, increased latency seemingly did not provide enough of an incentive to choose the correct direction in the first place, as although latency to retrieve the reward was shorter in block 2 compared with block 1 across all compliant conditions, this did not coincide with an improvement in performance in terms of correct initial choice of direction.

The fact that subjects always obtained the reward eventually, and did so with little penalty or additional effort following an initial error (other than it taking longer to retrieve the reward) perhaps meant that there was little incentive to choose correctly at the beginning of a trial (Call and Carpenter 2001). Kacelnik et al. (2006) suggested that the declining

performance of a New Caledonian crow (*Corvus moneduloides*) across consecutive testing sessions of the 'flimsy tool' problem may have been because she could choose again without penalty following an error. Alternatively, the subject may have had an inclination to explore the alternative option (Kacelnik et al. 2006). It is also possible that interacting with the apparatus may have been rewarding in itself, as has been suggested to be true for keas (*Nestor notabilis*; Miyata et al. 2011), chimpanzees (Clark and Smith 2013), and young children (Ellis and Siegler 1997).

Incentive and motivation could go some way to explaining capuchins' use of size to predict weight in Visalberghi et al.'s (2009) study. Transporting stones and nut-cracking is energetically expensive and time consuming (Massaro et al. 2012) compared with having to pull an alternative rake ('flimsy tool' problem; Povinelli et al. 2000), or roll a reward back in the opposite direction (this study). Visalberghi et al.'s (2009) study on the other hand provided subjects with a real incentive to make a correct decision regarding which stone to select in the first place. The same might be said about toddlers exploring the handrails in the study by Berger et al. (2005); the experiment exploited a real-life scenario, and there was likely a real perceived cost of falling if the handrail's properties did not provide sufficient support (though the experimenter obviously ensured the subjects' safety). Therefore, future studies should use paradigms that increase the incentive to choose correctly in the first place.

Fewer deliberate switches were made between barriers in block 2 compared with block 1, across all conditions. The latency to the first deliberate switch from one barrier to the other was also shorter in the second block. Switching is a form of error correction that may reflect a subject's decision-making process (Visalberghi et al. 2009). Although it can be difficult to determine if and/or when an animal is collecting perceptual information (Chappell et al. 2012), these findings suggest that subjects rapidly became more adept at interpreting the haptic feedback they received when they encountered a barrier with the reward, and how this related to whether or not it could be bypassed. For example, when

subjects pushed the reward against a non-compliant barrier, the feedback they received suggested that the barrier's affordances would not permit the creation of a functional gap that would enable the reward to bypass it, causing them to change the direction in which they moved the reward.

When Visalberghi et al. (2009) artificially manipulated the properties of stones so that smaller stones were heavier than larger stones, they found that the capuchins consistently selected heavier functional stones for nut-cracking. They did so by using appropriate exploratory behaviours that enabled them to infer the stones' affordances (Visalberghi et al. 2009). In this study, in the conflicting and same/different compliant conditions, compliance of the barriers could not be predicted accurately using diameter as a visual cue. The compliant properties of the barriers could however be extracted via the use of relevant exploratory procedures to directly experience their affordances. Therefore, under these conditions, having experienced the 'surprising' properties of the barriers, subjects might have been expected to use active testing behaviours to gain information about their affordances and use this information to guide future behaviour (Chappell et al. 2012). One subject (Silvia) regularly exhibited exploratory behaviour of the barriers. Her method of pushing against the barriers with her fingers was an appropriate exploratory procedure for extracting information about their compliance (Lederman and Klatzky 1987). She did this most frequently in the conflicting condition, where all of her explorations were of the thinner non-compliant barrier. This might suggest she understood something was 'wrong' and was attempting to extract information, like the capuchins tapping the artificial stones (Visalberghi et al. 2009), which may have contributed to her performing better than the other two subjects in this condition. On five occasions Silvia's haptic exploration of an incorrect barrier caused her to switch the direction in which she was moving the reward. This implies that her decision-making was influenced by information she extracted regarding the affordances of the barrier and the size of the functional gap that could be created, i.e. that it would not be possible to displace the barrier sufficiently for the reward

to pass under it.

Negative results of the type found in this study (i.e. a lack of evidence for a use of thickness as a visual predictor for compliance) are notoriously difficult to interpret (Seed et al. 2012). It has been argued that experiments based on contexts that are more ethologically valid may be more likely to reveal abilities such as those investigated here, should they exist (Seed and Tomasello 2010). However, one aim of using abstract, 'unnatural' tasks in a laboratory setting is to attempt to reveal whether animals possess general, transferable problem-solving abilities related to the capacity under investigation, as opposed a relatively inflexible ability that evolved in response to a specific challenge (Roth and Dicke 2005). Although captive orangutans did not use diameter to predict compliance in the problem-solving context they were presented with here, the possibility that wild orangutans use diameter as a visual cue to infer something about the compliant properties of supports during arboreal locomotion and nest-building cannot be ruled out. The fact that wild orangutans do not often fall from the canopy or reach arboreal 'dead-ends' implies that they must understand something about the compliant properties of arboreal supports, and such an ability would be expected to be under strong selective pressure. Furthermore, wild orangutans have been shown to select materials appropriate for different elements of nest building on the basis of diameter and structural properties (van Casteren et al. 2012), and there is experimental evidence that orangutans do understand the relevance of compliance in an experimental tool-using context (Manrique et al. 2010; Walkup et al. 2010). However, whereas in the wild branch diameter is a reliable and easily observable indicator of compliance (van Casteren et al. 2013), supports in captive environments have very different material properties, and thin artificial supports may still be rigid. Therefore, for captive orangutans diameter is not necessarily an accurate predictor of compliance. Also, as captive animals are likely familiar with all the supports that are available to them they have little need to be able to predict their properties (Phillips 2011). This is in stark contrast to a wild orangutan faced with a vast amount of information to process regarding

which supports are safe to utilise and which should be avoided. A less abstract, more ecologically valid avenue for further investigation might be to see how captive animals in a familiar environment would respond if novel supports varying in terms of their compliant properties were introduced into their enclosure.

In the final empirical chapter of this thesis (chapter 7) a unique opportunity was utilised to investigate orangutans' knowledge of compliance in a less controlled, more naturalistic setup than the previous study (chapter 6). In chapter 7, captive orangutans are confronted with novel horizontal supports in their locomotor environment, and I aim to examine how they explore and learn about their compliant properties, with a focus on their positional behaviour.

Chapter 7

HOW DO CAPTIVE ORANGUTANS (*PONGO ABELII*) LEARN ABOUT THE PROPERTIES OF NOVEL COMPLIANT SUPPORTS IN THEIR LOCOMOTOR ENVIRONMENT?

Abstract

Dealing with arboreal support compliance is a key challenge faced by large-bodied animals living in forest canopies, such as orangutans. Thin, fragile peripheral branches must be utilised to access ripe fruit and cross gaps between adjacent trees, which poses issues of safety and stability. Although a lot is known about orangutan locomotion and support use in the wild, to our knowledge the behaviour of orangutans when interacting with novel complaint supports has never been studied in captivity. We examined the positional and exploratory behaviour of five Sumatran orangutans (*Pongo abelii*) during their initial 4.5 hours of exposure to two novel horizontal supports: one with a diameter of 60 mm; and a second (more compliant) one with a diameter of 45 mm. Contrary to traditional theoretical preditions, large-bodied adults did not exhibit high frequencys of suspensory behaviour when initially interacting with either of the supports; rather they used multiple supports to avoid loading all of their weight onto a support with unknown compliant properties. Subjects rapidly engaged in appropriate exploratory procedures (e.g. bouncing at the tips of the supports) for extracting information about compliance. Calculating the force being applied during bouncing behaviour revealed that the maximum force that an individual applied during a bout increased with accumulation of time spent interacting with a support, presumably as individuals gained knowledge of a support's compliant properties and became more confident.

7.1 Introduction

Dealing with the compliant properties of arboreal supports has long been recognised as a key challenge for animals living in forest canopies (Grand 1972). Two key problems that need to be overcome are accessing edible items such as ripe fruit and crossing gaps in the canopy (Grand 1972; Cant 1992), both of which involve utilising thin peripheral branches where compliance (flexibility) is highest (van Casteren et al. 2013). Challenges associated with compliance are particularly pronounced for large-bodied animals such as orangutans (*Pongo* spp), because branches deform more under their mass compared with smaller bodied animals (Cant 1994). This increases the width of gaps to be crossed (Cant 1987) and also means that branches are less stable and more likely to break (Povinelli and Cant 1995; Thorpe et al. 2009).

Movement through a compliant arboreal habitat for a large-bodied animal is interesting from a cognitive perspective because it is an example of physical problem-solving that likely involves some form of planning as well as some knowledge of the invisible object property of compliance. Particularly during gap-crossing, orangutans must be able to predict how a branch will react to their own body weight before they move on to it and judge whether or not it is a suitable support to utilise. Chevalier-Skolnikoff et al. (1982) suggested that the key factor driving the evolution of orangutan intelligence may have been the requirement for locomotor solutions to such a complex arboreal habitat. Povinelli and Cant (1995) developed this idea, proposing that having to deal with problems caused by the combination of a large body and a fragile, compliant arboreal habitat drove the evolution of basic self-conception in a great ape ancestor, which enabled these animals to plan and execute complex locomotion necessary for safe and effective travel.

We know a good deal about orangutan locomotion and support use in the wild from detailed field studies (e.g. Thorpe and Crompton 2005; Manduell et al. 2011; Myatt and Thorpe 2011) and there is increasing evidence to suggest that orangutans may use

support diameter as a proxy for compliance in the wild, both in the context of locomotion (Thorpe and Crompton 2005, 2006) and nest building (van Casteren et al. 2012). A recent study has demonstrated that compliance is significantly correlated with living branch diameter (thicker branches are less compliant), as well as distance from the tip of a branch (compliance rapidly dissipates with increasing distance from the tip; van Casteren et al. 2013). Wild orangutans have also been observed to use support compliance to their advantage, by using their body weight to sway trees across gaps that are too wide to cross directly (Chevalier-Skolnikoff et al. 1982; Bard 1995). Thorpe, Crompton and Alexander (2007) demonstrated that tree-sway substantially reduces the energetic cost of crossing gaps, compared with jumping across, or descending to the ground and climbing back up on the other side of the gap.

In this study we utilised a unique opportunity to observe the behaviour of captive orangutans (*P. abelii*) interacting with novel compliant supports in their locomotor environment, to examine how individuals learn about compliance in this context. Orangutans need to be able to rapidly develop a good understanding of a support's affordances in order to use it safely and effectively. Novel objects trigger exploration, which enables individuals to actively gather information about them and learn about their physical properties, thus reducing uncertainty (Hughes 1997; Chappell et al. 2012). Exploration may be particularly important when an object's properties cannot be perceived via vision alone, as is the case for compliance (though branch diameter and compliance are correlated in the wild; van Casteren et al. 2013). Given that captive animals are generally very familiar with the properties of all of the supports in their enclosure, orangutans (particularly large-bodied adults) may be expected to act cautiously when confronted with a novel support. They might explore it visually on approach (Demery 2012) and then quickly engage in exploratory manipulation to extract information about its compliant properties. It is known that humans spontaneously carry out specific exploratory procedures that optimise the uptake of desired information about an object; for example, the application of force by pressing

or bending an object is commonly used to extract information about its compliance or hardness (Lederman and Klatzky 1987). Demery et al. (2010) argued that rather than being random, object exploration is targeted selectively and in a structured manner, according to the nature of the problem that an individual is confronted with. Pressing or bending would not be an appropriate exploratory procedure for extracting information about the compliant properties of novel locomotor supports because such behaviours would not exert sufficient force to reveal anything about their compliant properties. It seems more likely that subjects would manipulate the beams by loading their body mass on to them, causing them to deflect and hence reveal information about their compliance.

The aim of this study was to investigate the behaviour of captive orangutans on two novel horizontal supports that differed in terms of their diameter and compliant properties. One had a diameter of 60 mm and the second 45 mm, which are both within the range of support diameters commonly experienced by wild orangutans (Cant 1987). Orangutan behaviour was examined at the positional behaviour level, because typical object manipulation in terms of smaller scale movements (e.g. pushing or twisting with the hands) would not exert sufficient force to extract information about the compliant properties of the beams. It was also possible to measure force being applied by individuals during bouts of deliberate deformation (e.g. when they bounced on the supports causing them to deflect downwards), providing a unique insight that would not be possible to achieve in the wild.

Specifically, we aimed to test the following hypotheses:

1. Individuals (particularly large-bodied adults) should employ **high levels of suspensory positional behaviour when initially interacting with a novel beam**, because this increases their safety and stability, as the animal has, in effect, already 'fallen off' the support (Cartmill 1985; Cant 1994). Frequency of suspension should decrease over time as individuals learn that a beam will safely support their weight.
2. Individuals (particularly large-bodied adults) should **use additional supports**

when initially interacting with a novel beam, because multiple support use allows body mass to be distributed more safely compared with when only one support is used (Cant 1987; Thorpe and Crompton 2005; Thorpe et al. 2009) and reduces the risk of falling if different limbs are contacting different supports (Myatt and Thorpe 2011). Frequency of multiple support use should decrease over time as individuals learn that a beam will safely support their weight.

3. Individuals (particularly large-bodied adults) should exhibit **higher frequencies of (a) suspension, and (b) multiple support use on the 45 mm beam compared with the 60 mm beam**, given that diameter predicts compliance (van Casteren et al. 2013) and support diameter influences positional behaviour in the wild (Thorpe and Crompton 2005).
4. Individuals (particularly large-bodied adults) should exhibit **higher frequencies of (a) suspensory positional behaviour, and (b) multiple support use at the tips of the beams compared with the other sections** of the beams, given that the compliance experienced by an animal is affected by its position along a horizontal support and compliance rapidly dissipates with increasing distance from the free (unattached) end (van Casteren et al. 2013).
5. All individuals should **rapidly engage in appropriate exploratory behaviour** of the beams, as novelty induces exploration (Hughes 1997). Because the usual forms of exploratory manipulation for compliant objects (e.g. pushing or bending; Lederman and Klatzky 1987) would provide insufficient force to reveal anything about the beams' properties, exploration will likely take the form of individuals loading their body mass on to the beams and extracting information about compliance from the extent of their deformation. This loading might be expected to increase over time with accumulating experience of the beams' properties.

7.2 Materials and methods

7.2.1 Subjects and housing

Seven Sumatran orangutans (*P. abelii*) were housed in the enclosure at Chester Zoo, UK where this study was conducted: a flanged adult male, two adult females, two juveniles and two infants. As the two infants were difficult to distinguish and the beams did not deflect under their small body masses, they were not included in this study. Details of the five focal subjects from whom data were collected are shown in Table 7.1.

Table 7.1 – Study subjects: age-sex class, age in years, and weight

Subject	Age-sex class [a]	Age (years)	Weight [b] (kg)
Puluh	Flanged adult male	23	117.86
Emma	Adult female	22	59.56
Subis	Adult female	23	55.56
Budi	Juvenile male	6	22.56
Utara	Juvenile female	6	21.57

[a] Age-sex classifications follow Wich et al. (2004)

[b] Subjects were weighed when stationary on one of the beams

7.2.2 Apparatus: the compliant branch system

As part of a project investigating the mechanics of bipedal walking in orangutans, a compliant branch system consisting of a force sensor and a carbon fibre beam attached in a cantilever arrangement was mounted beneath a tunnel connecting the indoor and outdoor parts of the enclosure (Fig. 7.1).

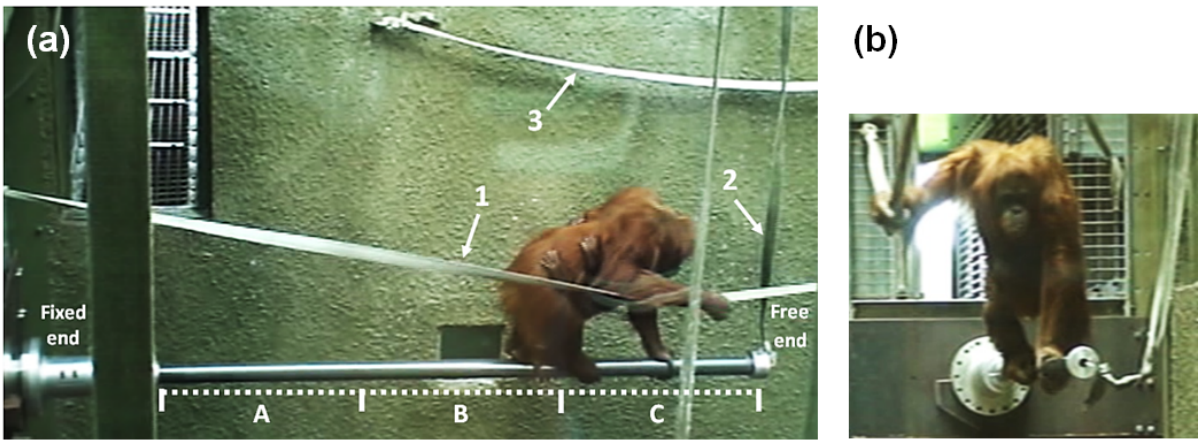

Figure 7.1 – (a) Photograph of compliant beam setup identifying the fixed and free ends and sections of the beam (A-C), as well as additional supports (1-3) that could be used be the subjects; and (b) a still taken from video showing the angle from which footage was recorded

Over a period of five months four different beams were installed, which were designed to replicate horizontal arboreal supports with different diameters and compliant properties. Beams were presented in order of decreasing diameter (100 mm, 80 mm, 60 mm and 45 mm) and each beam was present for five weeks. There were three additional supports (1-3 in Fig. 7.1a) that could also be used by the subjects in conjunction with the beam. This study examined behaviour of the orangutans during the first 4.5 hours of their exposure to the two narrowest beams (60mm and 45mm diameter) that were presented third and fourth. They had no prior experience of these supports. Information about the compliant properties of the two beams used in this study and the extent to which they would deflect at their tip under the weight of the focal individuals is given in Table 7.2.

Table 7.2 – Details of the compliant properties of the two beams used in this study and the expected downward deflection of their tips under the body mass of the five focal subjects

Beam diameter (m)	Beam length (m)	Flexural rigidity (Nm^2)	Expected deflection of tip of beam (m) under body mass				
			Puluh	Emma	Subis	Budi	Utara
0.060	2.587	26308	0.253	0.128	0.120	0.048	0.046
0.045	2.395	16759	0.316	0.160	0.149	0.060	0.058

7.2.3 Data scoring

All behaviour during interactions between the subjects and the beams was continuously recorded from video footage (see Fig. 7.1b for angle from which footage was recorded). This enabled all of the behaviour of each subject to be recorded in detail, and was necessary in order to capture infrequent behaviours such as deliberate deformation of the beams. Details of the data recorded are shown in Table 7.3.

Table 7.3 – Details and descriptions of data recorded

Data recorded	Description
1. Beam identity	60 mm diameter; 45 mm diameter
2. Subject	See Table 7.1
3. Positional behaviour category	Locomotion; posture; dynamic posture (posture involving movement, often repetitive, which does not involve travel)
4. Positional behaviour mode	*Locomotor modes*: Quadrupedal walk, tripedal walk, bipedal walk, orthograde forelimb suspend, forelimb-hindlimb swing, hindlimb swing; pronograde suspend (Hunt, 1996; Thorpe and Crompton, 2006; see Appendix C for detailed descriptions) *Postural modes*: Lie, sit/squat, orthograde stand; orthograde quadrumanous suspend, orthograde forelimb suspend, hindlimb suspend, forelimb-hindlimb suspend, pronograde suspend, pronograde stand (Hunt, 1996; Thorpe and Crompton, 2006; see Appendix C for detailed descriptions) *Dynamic postural modes*: sit/squat + bounce, tripedal stand + bounce, pronograde suspend + bounce, orthograde forelimb suspend + bounce, hindlimb suspend + bounce, pronograde suspend + swing, orthograde forelimb suspend + swing, hindimb suspend + swing (additional category for this study; see Appendix C for detailed descriptions)
5. Duration	Time in seconds for each positional behaviour mode
6. Support use	Beam only; beam plus 1 support; beam plus 2 supports; beam plus 3 supports
7. Section(s) of beam used for posture/ dynamic posture	A; B; C (see Fig. 7.1a)

Positional behaviour and support use

Positional behaviour was classified following Hunt et al. (1996), including additional modes described by Thorpe and Crompton (2006). This system records information

regarding how weight is borne (in suspension: below support; in compression: above support), trunk orientation (orthograde: upright trunk; pronograde: horizontal trunk), and which limbs are bearing weight. Prost (1965) categorised all positional behaviour as either posture or locomotion, with the two categories being mutually exclusive; the latter involving gross displacement of body mass in relation to the environment. For this study, the additional category of 'dynamic posture' was included, defined as posture involving movement, often repetitive, which did not involve travel. Dynamic postures were classified following Hunt et al. (1996), but included an additional component describing the dynamic aspect of the behaviour. Examples of dynamic postures include sit/bounce and pronograde suspend/swing (see Appendix C for detailed descriptions of dynamic postural modes). The key distinction from locomotion is that these behaviours do not involve moving from place to place (Prost 1965), for example along a support, but may involve moving around a fixed location, for example swinging from side to side beneath a support without travelling along it. Dynamic postures may be of particular interest in the case of novel locomotor supports in a captive setting, as they tend to exert more force than locomotion and posture and might therefore be related to exploratory behaviour, and 'testing' of the beams' affordances.

For each positional behaviour mode recorded, information about the use of additional supports (1-3 in Fig. 7.1a) was also recorded (Table 7.3); specifically whether the beam was the only support being used, or whether additional supports were also being used, either for weight-bearing or balance. A subject's position along the beam was also recorded (A, B, C in Fig. 7.1a; Table 7.3).

Force applied during deliberate deformation of supports

During bouts of dynamic posture subjects sometimes deliberately deflected the beam using their own body mass (e.g. by sitting and bouncing). When a subject was positioned at the tip of a beam it was possible to calculate the force they were applying. (As it was

not possible to accurately ascertain the position of an individual mid-way along beam due to angle from which video footage was recorded (see Fig 7.1b), and a subject's position along the beam (L in Fig. 7.2) was key to calculating force, force calculations could not be carried out when subjects were positioned elsewhere on the beam). Force applied at the free end of the beam was calculated by measuring the beam's maximum vertical deflection and calibrating it based on the weight of the subject (Table 7.1). The videos were scaled based on the known diameters of the end plates of the beams. For each bout of deliberate deflection, the maximum vertical deflection of the beam was measured in pixels using ImageJ, and converted into metres. The force being applied could then be calculated using the equation in Fig. 7.2.

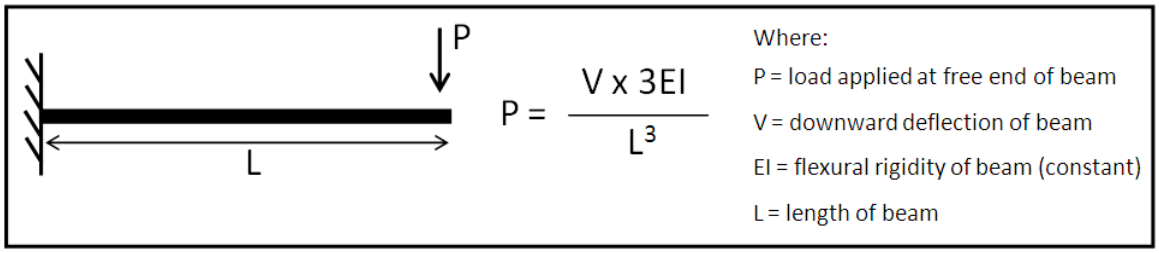

Figure 7.2 – Force applied at the free end of the beam (P) was calculated based on knowledge of the weight of the individual, the length of the beam (L), how much it deflected (V), and the flexural rigidity of the beam (EI; see Table 7.2)

7.2.4 Data analysis

Due to the small sample size, and based on theoretical predictions regarding suspension as a 'safe' behaviour on compliant supports, positional behaviour was conflated to the following categories: suspensory locomotion, suspensory posture, suspensory swinging, suspensory bouncing, compressive locomotion, compressive posture, compressive bouncing. In some cases these categories were conflated further, to suspension vs. compression, to enable meaningful analyses to be conducted. For the same reason, support use was conflated to beam only vs. beam plus additional support(s). The distinction between single and multiple supports was found to be the most meaningful way of interpreting

number of supports used by Thorpe and Crompton (2005). Position along the beam was also conflated to fixed end (sections A and B) vs. free end (section C; Fig. 7.1a) since compliance rapidly decreases with increasing distance from the tip of a horizontal support (van Casteren et al. 2013).

To enable detailed qualitative examination of behaviour, we plotted (a) positional behaviour and (b) support use minute-by-minute for each subject. Chi-square tests were used to compare frequency of suspension vs. compression (hypothesis 1) and single vs. multiple support use (hypothesis 2) between the first minute of interaction with a beam and subsequent time spent interacting with it. Chi-square tests were also used to look for differences in frequencies of suspension vs. compression and single vs. multiple support use between the two different beams (hypothesis 3), and between the fixed vs. free end of each beam (hypothesis 4). In each case adults and juveniles were examined separately to investigate the effects of body size on positional behaviour. Where sample sizes were particularly small resulting in more than 20% of cells in contingency tables having expected frequencies of less than 5, Fisher's exact test was used instead of a Chi-square test, as it is appropriate for examining the significance of associations regardless of sample characteristics. Finally, to examine exploratory behaviour (hypothesis 5), for each subject that performed multiple bouts of deliberate deformation at the tip of a beam we measured the maximum force applied during each bout and plotted this against an individual's time spent interacting with the beam.

7.3 Results

Across all five focal subjects, the amount of time spent interacting with the 60 mm beam within the first 4.5 hours of the beam being present was 3364 seconds. There was less interaction with the 45 mm beam following its introduction: a total of 1139 seconds in the first 4.5 hours. There was high inter-individual variation in the extent of beam interaction. Table 7.4 shows the frequencies of the three categories of positional behaviour recorded for

each subject on each beam, as well as the total duration each subject spent interacting with each beam.

Table 7.4 – Summary of the frequency of positional behaviour recorded for each subject on each beam, and the total duration each subject spent interacting with each beam. Fz is the total frequency of behaviors recorded (loco + posture + dynamic posture)

Subject	60 mm beam			Totals		45 mm beam			Totals	
	Loco	Posture	Dynamic posture	Fz	Duration (s)	Loco	Posture	Dynamic posture	Fz	Duration (s)
Puluh	8	5	0	13	101	7	0	1	8	34
Emma	24	104	31	159	1766	11	16	10	37	350
Subis	6	8	4	18	151	2	1	0	3	11
Budi	52	62	31	145	1093	32	51	18	101	562
Utara	4	15	0	19	253	8	16	1	25	182

7.3.1 Positional behaviour and support use

Fig. 7.3 and Fig. 7.4 show each focal subject's positional behaviour and support use minute-by-minute for all of the time they spent interacting with each beam.

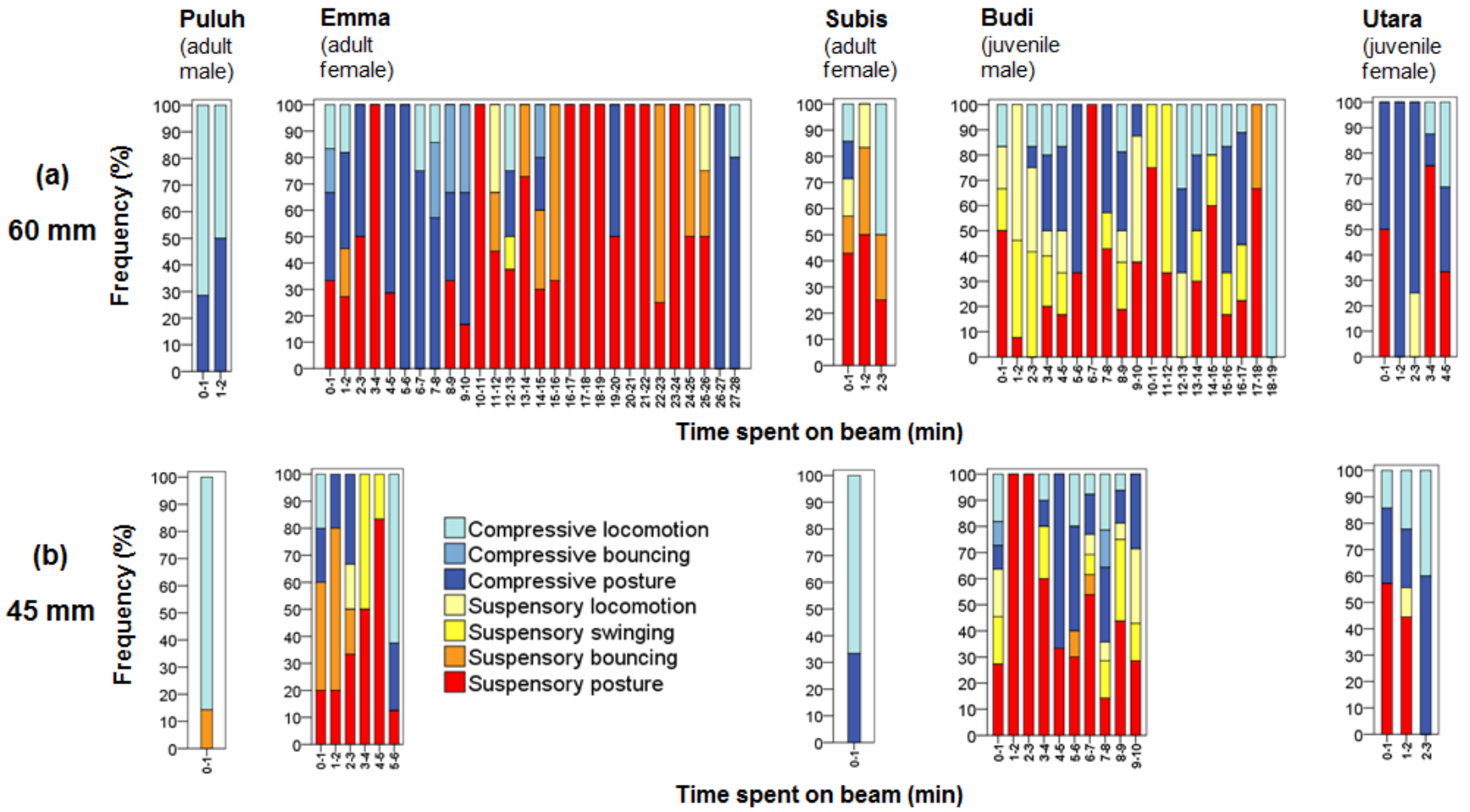

Figure 7.3 – Minute-by-minute positional behaviour for each subject on each beam, covering all of the time they spent interacting with each beam. N.B. durations are cumulative rather than continuous, i.e. some subjects left the beam and returned to it multiple times within the 4.5 hour period of observation. The red through to pale yellow spectrum represents suspensory positional modes and the dark blue to pale blue spectrum represents compressive modes

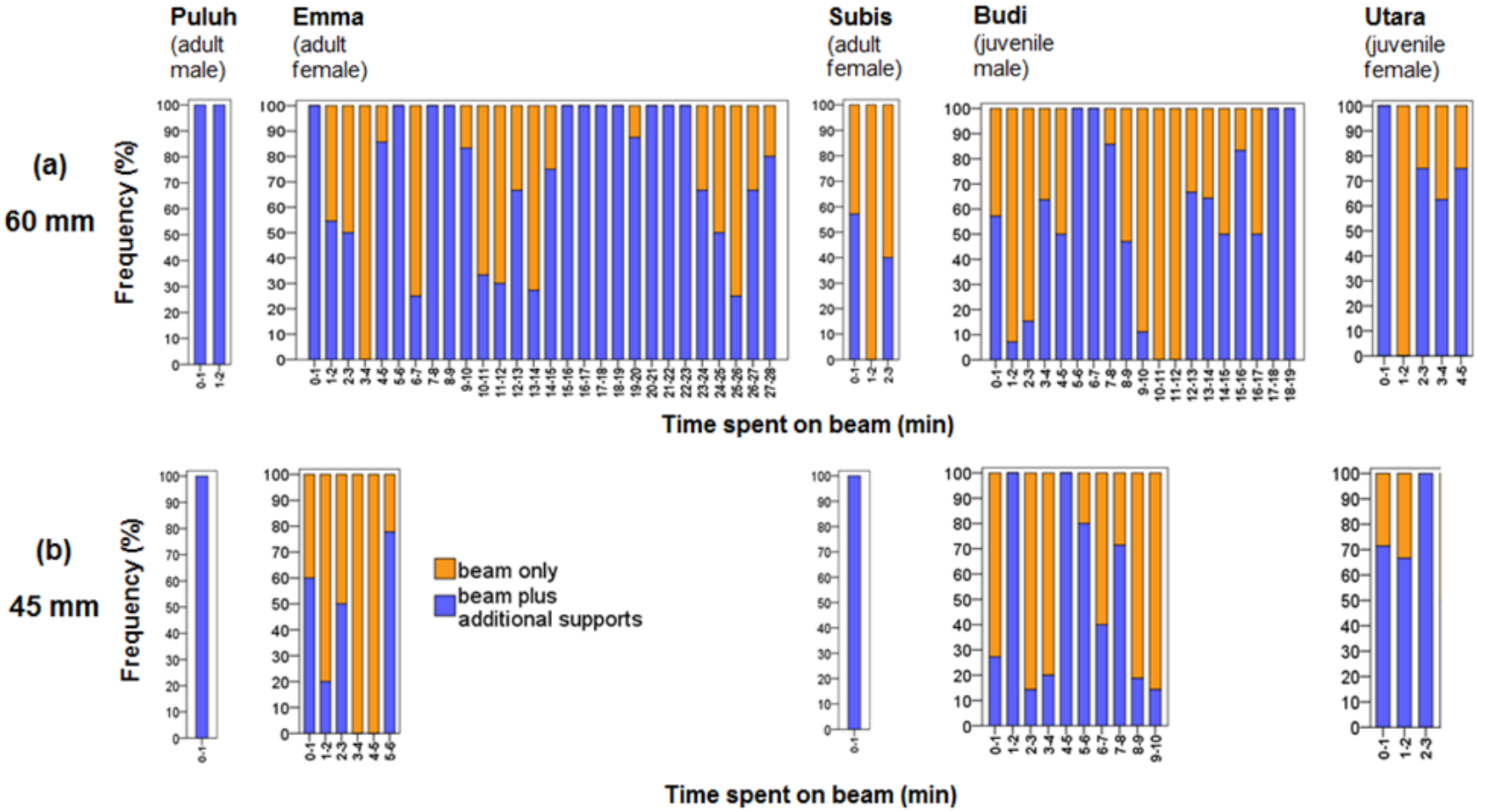

Figure 7.4 – Minute-by-minute support use for each subject on each beam, covering all of the time they spent interacting with each beam. N.B. durations are cumulative rather than continuous, i.e. some subjects left the beam and returned to it multiple times within the 4.5 hour period of observation. Orange represents positional behaviour modes where the beam was the only support involved and blue represents modes where multiple supports (beam plus any of the additional supports (1-3 in Fig. 7.1a) were used

Adults exhibited significantly less suspension in their first minute spent interacting with the 45 mm beam than in their subsequent time on that beam (Table 7.5). Although the data for the 60 mm beam showed the same pattern, the result was not significant (Table 7.5).

Table 7.5 – Comparison of behaviour during the first minute of interaction with the beams (1st min) and the remainder of time spent interacting with the beams (subsequent) for adults and juveniles in terms of the frequency of (a) suspension vs. compression and (b) multiple vs. single support use. – indicates Fisher's Exact test was used due to expected cell frequencies of less than 5

Beam	Age	(a) % suspension				(b) % multiple support use			
		1st min	Subsequent	χ^2	*P*	1st min	Subsequent	χ^2	*P*
60 mm	Adult	35.0	51.9	2.031	0.154	85.0	68.2	2.943	0.086
	Juv	75.0	63.4	-	0.712	66.7	49.1	-	0.323
45 mm	Adult	13.3	66.7	11.383	**0.001**	86.7	53.3	10.045	**0.002**
	Juv	61.1	61.4	0.000	0.982	44.4	48.3	0.128	0.720

For juveniles on the other hand the frequency of suspensory behaviour did not differ between their initial minute of interaction and overall time spent on either of the beams (Table 7.5). Adults also used multiple supports more frequently in their initial minute on the 45 mm beam than overall and showed the same (non-significant) pattern on the 60 mm beam (Table 7.5), whereas for juveniles support use did not differ between the first minute and subsequent time spent on either of the beams (Table 7.5).

Overall, juveniles exhibited significantly more suspensory behaviour than adults on the 60 mm beam (Table 7.5; χ^2_1=6.577, p=0.010). Overall frequencies of suspension vs. compression did not differ between adults and juveniles on the 45 mm beam (χ^2_1=2.079, p=0.149). Significantly more behaviour exhibited by adults on the 60 mm beam involved the use of multiple supports compared with juveniles (Table 7.5; χ^2_1=12.903, p<0.001). Adults and juveniles did not differ in terms of support use on the 45 mm beam (χ^2_1=0.327, p=0.567).

Between-beam comparisons of behaviour revealed no significant differences in frequency of suspension vs. compression (Fig. 7.3 and Fig. 7.5), or single vs. multiple support use (Fig. 7.4 and Fig. 7.6), for either adults or juveniles (Chi-square tests, $p>0.05$ for all).

Behaviour was generally focused at the tips of the beams (section C in Fig. 7.1a); except for juveniles on the 60 mm beam; see Fig. 7.5aii). There were no significant differences between the frequency of suspension vs. compression at the fixed end compared with the free end of either of the beams for either adults or juveniles (Fig. 7.5; Chi-square tests, $p>0.05$ for all).

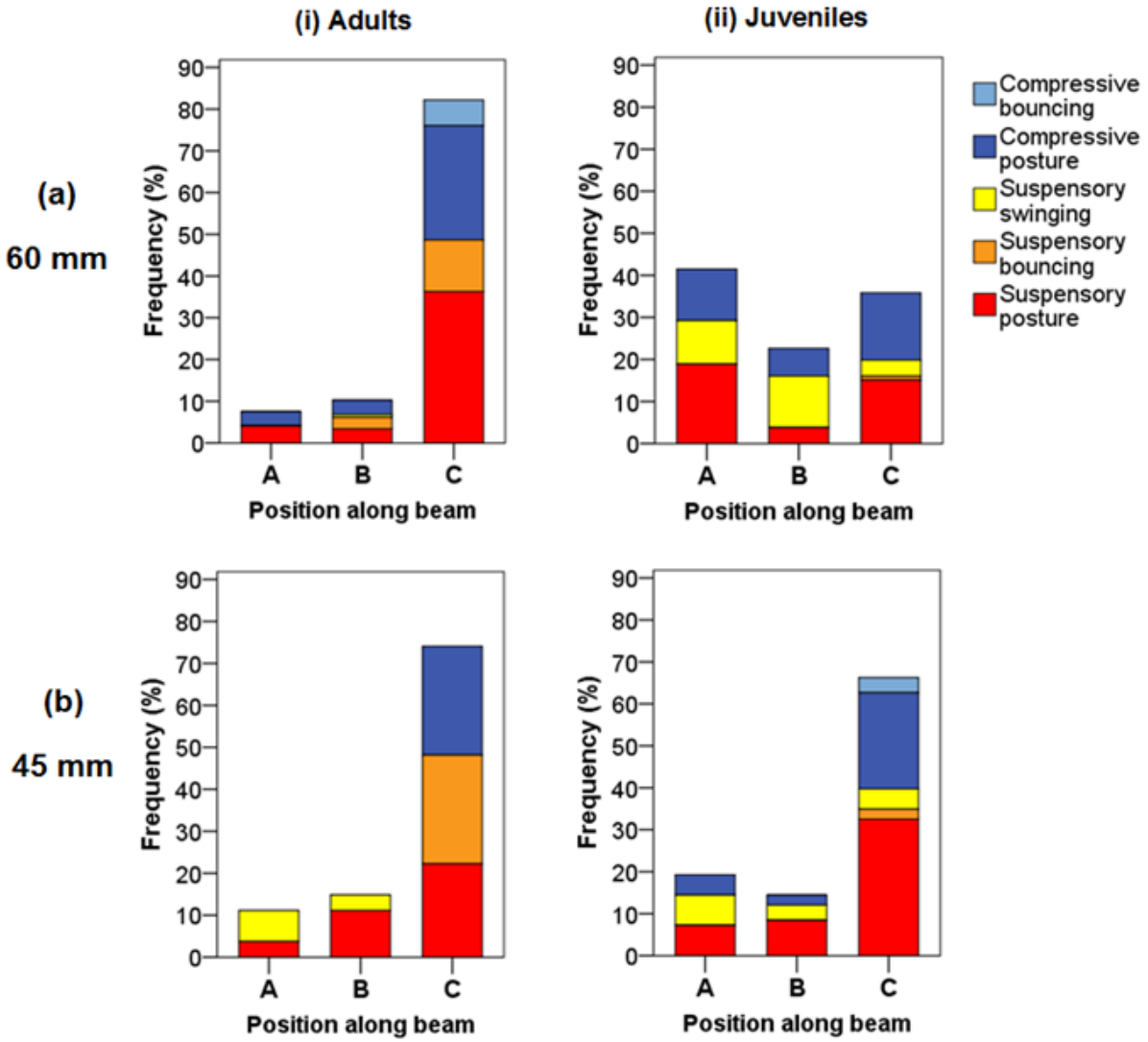

Figure 7.5 – Positional behaviour (excluding locomotion) at different positions along each beam for adult and juvenile subjects

Adults were significantly more likely to use multiple supports at the free end of the 60 mm beam compared with the fixed end (χ^2_1=22.949, p<0.001; Fig. 7.6ai), whereas there were no associations between beam section and support use for juveniles (p>0.05; Fig. 7.6aii). On the 45 mm beam, both adults and juveniles used multiple supports more frequently at the free end compared with the fixed end (adults: χ^2_1=7.000, p=0.008; juveniles: χ^2_1=22.596, p<0.001; Fig. 7.6b).

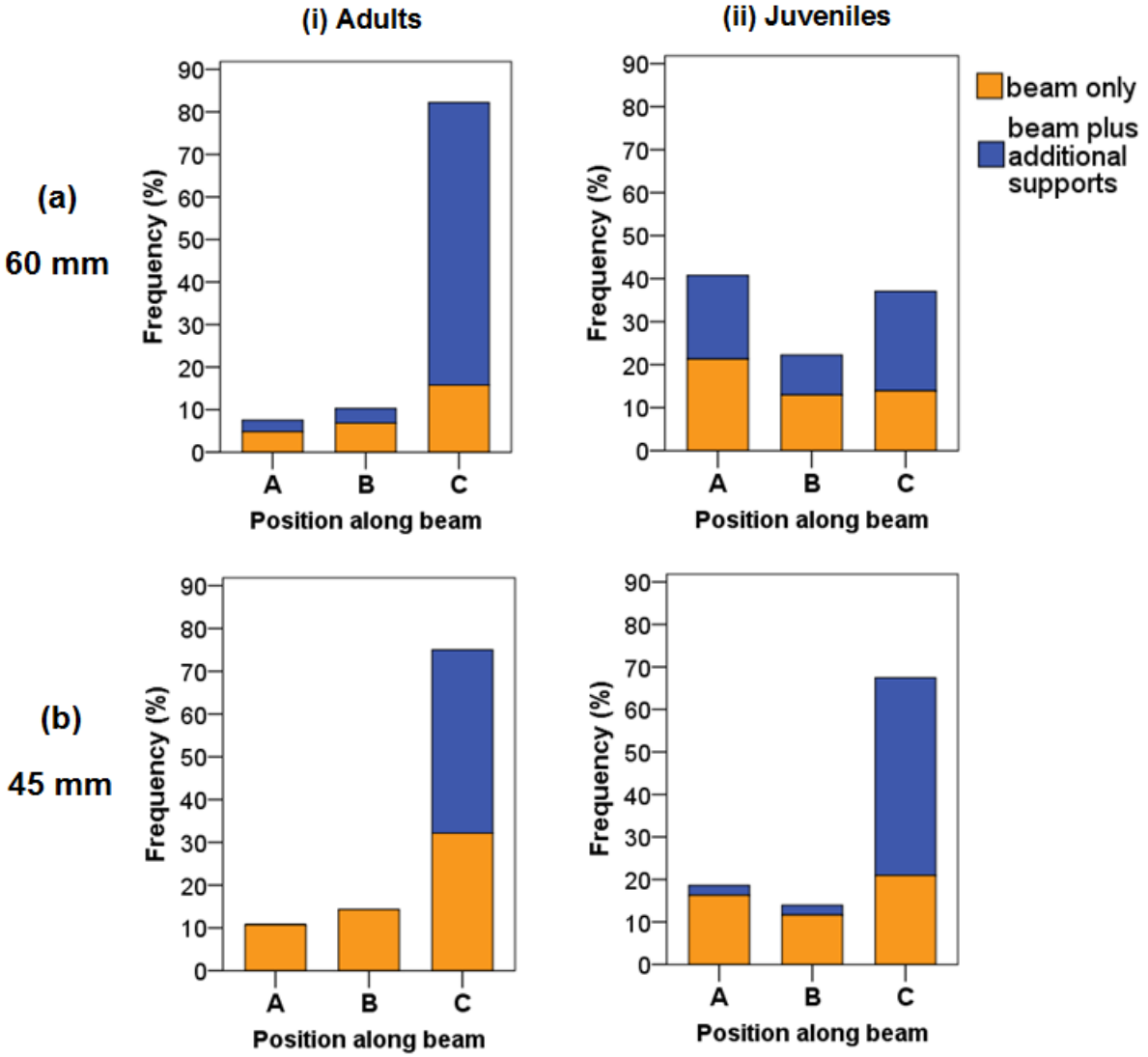

Figure 7.6 – Support use at different positions along each beam for adult and juvenile subjects

7.3.2 Deliberate deformation of supports

Both of the adult female subjects exhibited deliberate deformation of the 60 mm beam within their first minute spent interacting with it (Fig. 7.3). On the 45 mm beam three out of five focal subjects (Puluh, Emma and Budi) exhibited deliberate deformation within their first minute of interaction (Fig. 3). Deliberate deformation (compressive and suspensory bouncing) was focused at the free end of both beams (Fig. 7.5).

Fig. 7.7 shows that for bouts of deliberate deformation where it was possible to measure the maximum force being applied to the beam by a subject because they were positioned at the tip, there was a pattern of increasing maximum application of force with accumulation of time spent interacting with a beam.

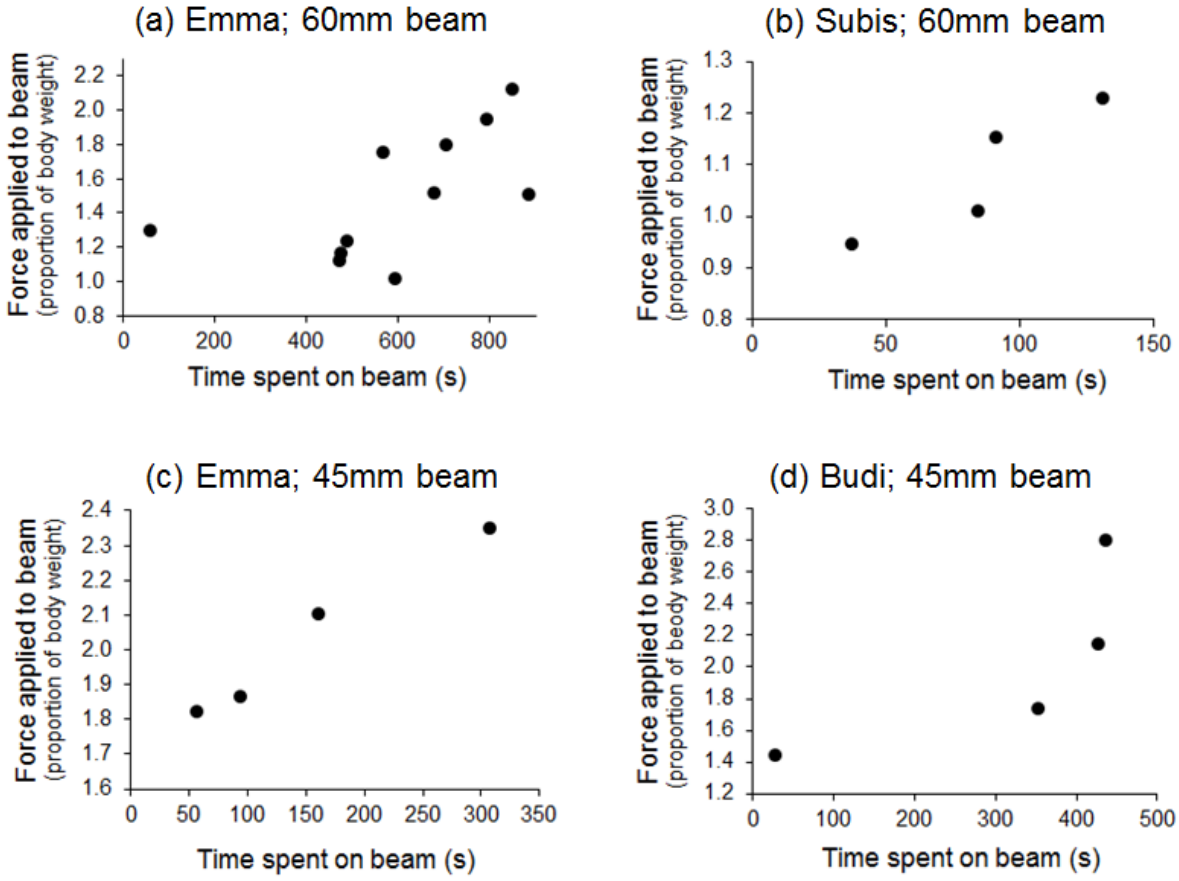

Figure 7.7 – Scatterplots showing the maximum force applied to the free end of a beam during successive bouts of compressive or suspensory bouncing. N.B. durations are cumulative rather than continuous, i.e. some subjects left the beam and returned to it multiple times within the 4.5 hour period of observation

There was inter-individual variation in how much force subjects applied to the beams in terms of proportion of body weight. Budi applied the greatest force during deliberate deformation: 2.8 times his own body weight in his final measurable bout on the 45 mm beam (Fig. 7.7d), generating a downward deflection of the tip of approximately 0.169 m. Emma and Subis' maximum force applications were 2.35 times (a 0.375 m deflection; Fig. 7.7c) and 1.23 times (a 0.147 m deflection; Fig. 7.7b) their body weights, respectively.

7.4 Discussion

This study provided a unique opportunity for detailed examination of how captive orangutans behave when confronted with novel horizontal supports with unknown compliant properties. Being able to measure the force individuals were applying to the beam provided a particularly interesting insight that it would not be possible to obtain through studies in the wild.

The captive environment is far less complex than the forest canopy and captive animals are generally familiar with the properties of all of the supports in their enclosure. It therefore seems reasonable to expect that orangutans – especially large-bodied adults – might behave cautiously when confronted with novel supports with unknown properties. Contrary to theoretical predictions (e.g. Grand 1972; Cartmill 1985; Cant 1994) we found no evidence for high initial levels of suspension; instead, adults seemed to select compressive modes and utilise multiple supports during their initial minute of interaction with the beams. This is more in keeping with the findings of Thorpe, Holder and Crompton (2007), which showed that forelimb-assisted compression was used on the narrowest supports by wild orangutans, because it increases stability in a complex, compliant habitat.

Orangutan positional behaviour conflated to suspension or compression did not differ between the fixed end and the free end of the beams; but there were differences in terms of the number of supports being used at these positions. Given that compliance decreases

rapidly with increasing distance from the tip (free end) of a horizontal support (van Casteren et al. 2013), it makes sense that orangutans should employ a strategy of using multiple supports at the free end of the beams, where they are most compliant. Adult orangutans selected positional behaviour involving multiple supports at the free end of both beams, whereas juveniles were only more likely to use multiple supports at free end of 45 mm beam. This is likely because the effect of body mass rendered the 60 mm beam more compliant under the adults than the juveniles (the tip deflected approximately twice the distance under the weight of the adult females compared with the juveniles), and may also relate to the more cautious nature of adult females compared with immature individuals (Thorpe and Crompton 2005).

Adults tended to rapidly engage (often within their first minute of interaction) in exploratory behaviour in the form of deliberate deformation of the beams. Orangutans have been shown to be relatively neophilic and bold compared with other apes, based on latency to approach novel items (Herrmann et al. 2011). Dynamic posture in the form of bouncing is an appropriate exploratory procedure to employ because it places a higher force on a support than locomotion or posture, and therefore maximises information gain in terms of the invisible feature of compliance. This behaviour mainly occurred at free end of beam, which may be indicative of the selectiveness of exploration (Demery et al. 2010), in which individuals target particular features of the novel object; in this case the most compliant section of the beam.

Three subjects (Emma, Subis and Budi) exhibited multiple bouts of deliberate deformation at the free end of one or both of the beams. The maximum force applied increased with subjects' accumulating experience of the beams properties, presumably as they became more confident that they would not break. Budi applied a force of almost three times his own body weight to the free end of the 45 mm beam, whereas adult females were less forceful when performing similar behaviours, which may again be related to the fact that wild juvenile orangutans are known to exhibit more risky locomotion than their mature

counterparts (Thorpe and Crompton 2006).

The juvenile male in this study exhibited a relatively high frequency of suspensory swinging, which appeared to be a form of play behaviour. Spinka et al. (2001) hypothesised that play is 'training for the unexpected', which is often triggered by novel stimuli, and occurs when individuals are able to explore actions in a low-risk setting (Buchsbaum et al. 2012; Chappell et al. 2012). It is related to exploration and serves to help animals develop flexible responses to cope with unexpected situations, such as falling due to a loss of balance (Spinka et al. 2001). In the present study, during bouts of suspensory swinging Budi would sometimes release his hands or feet from the beam mid-swing (Tecwyn, personal observation), seemingly deliberately putting himself into a risky situation. This 'self-handicapping' behaviour is thought to further enable the development of novel responses to unexpected circumstances (Spinka et al. 2001).

There was little evidence for differences in behaviour between the two beams. Visual exploration of a support's diameter may play a more important role when a support is out of reach and therefore cannot be explored via direct manipulation, which is often the case during gap-crossing in the forest canopy, but was not the case here. It is also possible that the sample size was too small to detect a difference in positional behaviour repertoire between the beams, or that subjects were more confident on the 45 mm beam (despite it being more compliant) having previously been exposed to the 60 mm beam and the two thicker beams. We could also not eliminate the possibility that the focal individuals had previous experience of similar supports, though they are uncommon in captive environments.

Neither of the beams was as narrow or compliant as the narrowest supports encountered in the wild (for obvious safety reasons), so it is possible that they were not particularly challenging for the orangutans, though they did deflect several centimetres at the tip, even under the weight of the juveniles. Furthermore, the beams were only 2 metres off

the ground, so it could be that the orangutans did not perceive a significant safety risk associated with falling.

To summarise, this study adopted a unique approach to investigate how captive orangutans learn about the properties of novel supports in their locomotor environment. In their initial minute of interaction, adults utilised compressive positional behaviour and used multiple supports to increase safety and stability on a narrow horizontal support with unknown compliant properties. They continued to use multiple supports at the free ends of the beams where compliance was highest. Several subjects (adult females and the juvenile male) deliberately deformed the beams by bouncing on them, particularly at the free end, which was an appropriate exploratory procedure for gaining maximum information about compliance. Furthermore, the force they applied increased as they gained experience of the beams' affordances and became more confident.

It seems that orangutans' boldness when confronted with novelty and rapid engagement in appropriate exploratory procedures enables them to quickly learn about the compliant properties of novel supports, and therefore adopt safe and effective positional behaviour.

Chapter 8

GENERAL DISCUSSION

The aim of this thesis was to expand our understanding of (1) the ability of great apes to plan during physical problem-solving, and (2) how they might predict and explore the 'invisible' compliant properties of objects. Both of these aspects of cognition are particularly relevant to challenges faced by great apes in the physical environment, especially orangutans. Specifically, wild orangutan behaviour in the context of arboreal locomotion and nest-building suggests an ability to consider alternative possible actions, plan of appropriate sequences of actions, and select supports with appropriate compliant properties. The research in this thesis investigated great apes' ability to plan, and their understanding of object compliance, by presenting captive individuals with novel problem-solving tasks (chapters 2 - 6) and novel objects (chapter 7), and observing their decision-making and behavioural responses.

When developing novel tasks, I aimed to bear in mind the challenges associated with designing physical cognition tasks (as outlined in section 1.7 of chapter 1), particularly those that could potentially be used to test multiple species, including non-tool users. The pieces of apparatus that I developed – the puzzle-tube (chapters 2 and 6) and the paddle-box (chapters 3, 4 and 5) – both fit many of the criteria that MacLean et al. (2012) have suggested would be appropriate for broad comparative studies. They were both easy to implement and as subjects required minimal training, they rapidly entered the testing phase (which is particularly important when working in zoos under time constraints). Both pieces of apparatus also had an adjustable level of difficulty. The number of gaps, traps and barriers could be varied and the obstacles could be combined in different ways in the puzzle-tube. The difficulty of the paddle-box could be adjusted in multiple ways: by requiring subjects to perform particular actions before turning the start paddle (i.e. the advance planning task); by altering the level at which the reward started; and by designing configurations in which success required the start paddle to be turned away from the goal.

I am by no means claiming to have eliminated the issues associated with investigating

physical cognition; there is still a very long way to go. Like many others before me, I faced the challenge of interpreting negative results (all ape subjects in the advance planning and compliant barriers tasks, and some subjects in all other tasks), and trying to decide whether these were due to an absence of the cognitive ability being investigated, peripheral processes being simultaneously taxed, numerous contextual variables influencing performance, rearing history, and/or the possibility that the task being presented was inappropriate.

One key issue in my opinion is a captive animal's incentive to get it right the first time, or in the case of planning tasks, motivation to plan before acting. None of the apes in this thesis were food-deprived prior to testing, and they received multiple consecutive trials, so had lots of chances to get rewards. This is of particular concern in tasks where the reward never became trapped so a reward is retrieved in every trial regardless of whether a subject 'succeeded', such as in the compliant barriers task (chapter 6). This could be rectified by modifying the apparatus so that at either side of the reward's central starting position there was a one-way flap, so that once a direction was selected the reward could not be moved back in the other direction (though error correction can in fact be a window onto decision-making processes). This issue of correctibility was addressed with the paddle-box apparatus because actions were not reversible as the reward could only move down through the puzzle. However, there was no real cost of failure other than losing a small (albeit desirable) food reward.

There is evidence that increasing the cost of performing a task in terms of effort required can alter the performance of apes. Martin-Ordas et al. (2012) found that apes had a preference for retrieving and using the longest tool out of a set of four in a sequential tool use task, regardless of the distance over which a reward had to be retrieved. While this is an appropriate strategy for success, it does not reveal anything about whether any planning might be involved in tool selection. When the cost of retrieving the longest tool was increased, so that the only way of accessing it was by using three increasingly long

tools in sequence, apes started to pay attention to the distance over which the reward had to be retrieved and select a shorter tool if appropriate (Martin-Ordas et al. 2012). Bottlenose dolphins also switched to a more efficient problem-solving strategy in a tool using task when the energetic cost of their preferred technique was increased (Kuczaj et al. 2009).

This issue of incentive to get it right in the first place is one benefit of carrying out experiments in the field, where animals are more likely to be motivated by energetic considerations and competition with conspecifics. Furthermore, seeing what animals actually do in the 'real world' can shed light on the selection pressures that drove the evolution of their cognition (Healy and Hurly 2003). But while studies of cognition in the wild seem to be increasing in a diverse range of species (e.g. Keagy et al. 2009; Visalberghi et al. 2009; Müller 2010; Benson-Amram and Holekamp 2012; Thornton and Samson 2012; Healy and Hurly 2013), to date there have been very few field experiments involving wild apes (but see Grüber et al. 2009), probably due to logistical and safety concerns.

8.1 Summary of main findings

8.1.1 Planning in the context of physical problem-solving

The results presented in chapter 2 (puzzle-tube with multiple obstacles) suggest that at least some orangutans were able to consider the effect of multiple obstacles (gaps, traps and end pieces) on the path of a food reward, and select the correct direction in which to move the reward out of two alternative possibilities. This task still had the issue of trial success being based on a binary choice (i.e. move the reward left or right). Furthermore, post-hoc analyses revealed that it was possible to succeed by using a series of procedural rules. However, even if this was how success was achieved (by Amos), these procedural rules were used flexibly and successfully from the first testing block, and were based on functionally relevant components of the task. Although the sample size for this study was

small, it permitted me to examine variation between individuals in detail. Rather than being satisfied that at least one subject succeeded and ignoring data from those who failed, I examined the performance of each subject to gain insight into what strategies each of them may have been using when attempting to solve this novel task.

Chapter 3 demonstrated that the majority of orangutans and bonobos tested were able to perform an appropriate sequence of actions in a step-by-step manner (sequential planning paddle-box task). However, all of the ape subjects tested failed to plan and execute appropriate actions in advance of acting on the food reward (advance planning task). High inhibitory demands related to the salience of the food reward were highlighted as a possible cause of failure in this task (i.e. the inhibitory demands of the task may have posed a cognitive load in addition to the planning demands, as tool use was found to do in Seed et al.'s (2009b) trap-tube study with chimpanzees). It has been demonstrated that replacing food with tokens in the reversed contingency task enables subjects to inhibit the strong behavioural predisposition to select the larger quantity (Boysen and Berntson 1995; Boysen et al. 1996; Kralik et al. 2002; Albiach-Serrano et al. 2007; Addessi and Rossi 2011). Consequently it could be argued that one way to probe the contribution of poor inhibitory control to failure in experiment 1 would be to pre-train subjects to exchange tokens for food, and then use tokens instead of food in the paddle-box.

While testing apes with tokens in the advance planning paddle-box task was not possible in this thesis, it was possible to investigate the impact of replacing reward items with tokens on the performance of children (chapter 4). Surprisingly, children in all three age groups tested did not perform better when their task was to retrieve a piece of sponge (token) from the paddle-box, compared with children whose task it was to retrieve a desirable sticker. Although the possibility remains that using tokens would improve the performance of apes, there is evidence from studies with other primates that tokens are only effective if they have a 'high-symbolic distance' (Addessi and Rossi 2011) from the reward (i.e. are a more abstract representation of the real food). For example, when individual food

items were replaced with rocks ('low-symbolic distance' tokens) two chimpanzees still struggled to inhibit picking the larger quantity (Boysen et al. 1996), but when the food arrays were replaced with Arabic numerals representing a particular quantity of food ('high-symbolic distance tokens'), performance improved significantly (Boysen et al. 1996). With the paddle-box, tokens can only be of 'low-symbolic distance', as although they would remove the immediate presence of food, the quantity salience (i.e. one token = one food item) would be retained, so the impact this would have on performance remains equivocal. Therefore, while inhibitory control may have some influence on the performance of children and apes in the advance planning paddle-box task, in the case of 4- to 10-year-old children it does not seem to be the key factor limiting performance.

The paddle-box proved to be an appropriate paradigm for testing the planning abilities of young children, because they had no difficulty understanding and following the limited verbal instructions unlike in some commonly used tasks (e.g. ToL), and there were clear developmental trends in performance. The way in which they approached the advance planning task also revealed interesting differences in problem-solving strategies between age groups.

The fact that adult humans did not perform perfectly in the advance planning paddle-box task (chapter 5) shows that it is not a trivial task, and highlights the fact that assumptions should not be made when interpreting the performance of animals. Some adults even moved paddles that were irrelevant to solving trials, though they did this less frequently when under time pressure, suggesting that when given unlimited time they tended to 'play it safe'.

8.1.2 Compliance in the context of physical problem-solving

The findings regarding orangutans' knowledge of the compliant properties of objects were somewhat ambiguous. There was no evidence that diameter was used as a visual cue to predict the compliant properties of barriers partially blocking passage of a food reward

(chapter 6). This does not however preclude the possibility that this strategy is used in the wild to predict the compliant properties of arboreal supports; based on observations of wild behaviour this still seems likely (e.g. Thorpe and Crompton 2005; van Casteren et al. 2012). It is also known that orangutans can select tools with appropriate compliant properties in a tool-using context (Walkup et al. 2010; Manrique et al. 2010). This study also raises concerns regarding the subjects' incentive to choose the correct initial direction (as discussed at the start of this chapter), rather than choosing randomly, and then if that does not work, try the other option. Further research in a more ecologically relevant context is required to further explore apes use of diameter to predict compliance. An interesting finding from this study was that the one subject who frequently explored the barriers (Silvia) used the information she extracted to guide her behaviour. For example, she would use her finger to push against the barrier she was moving the reward towards, and if the barrier was not compliant she would change the direction in which she was moving the reward (*before* it came in to contact with the non-compliant barrier) to push it towards the alternative barrier. This suggests that exploration may be important for extracting information about object properties that cannot be directly perceived using vision.

Further evidence for the importance of exploration in understanding compliance was observed in chapter 7, where orangutans were presented with novel horizontal locomotor supports. Several individuals rapidly engaged in relevant exploratory procedures for extracting information about compliance (e.g. bouncing), and this behaviour was focused at the highly compliant tips of the beams. Interestingly, the subjects in this study did not employ 'safe' (according to theoretical predictions) suspensory positional behaviour when initially interacting with these novel supports; rather they opted for an alternative safe strategy of using multiple supports so that they were not putting their entire mass onto a support with unknown properties.

8.2 Ideas and recommendations for future research

8.2.1 Locomotor support selection experiments

While carrying out experiments to investigate apes' planning ability and knowledge of object compliance in the field might prove too logistically challenging (particularly with highly arboreal orangutans), more ecologically relevant experiments (i.e. in the context of locomotion and nest-building) could be conducted in captivity. The compliant locomotor support setup used in chapter 7 could be extended to examine the use of diameter as a cue for predicting compliance, as well as the ability to consider alternative possible actions. A choice between two or more supports could be presented, where only one support would have appropriate compliant properties to afford access to an out-of-reach reward. For example, a reward might be suspended from the ceiling centrally above the ends of two horizontal supports: one twice as thick as the other. The thinner support would deform downwards under the weight of the subject so much that the reward could not be reached. The thicker support would be less compliant and deform less so that the reward would be obtainable when the subject was positioned at its tip. The compliant properties of the supports could also be confounded, like the barriers in the puzzle-tube in chapter 6; and the setup could be configured so that subjects had to use the more compliant support to access a reward.

8.2.2 Ape vs. monkey comparative work

In the introduction to this thesis I suggested that planning during physical problem-solving and knowledge of 'invisible' compliant properties of objects may have been selected for due to challenges in the physical environment uniquely faced by great apes (technical intelligence hypothesis; Byrne 1997), but it was not possible to address this question directly in this thesis. To date there have been relatively few systematic comparisons of great ape and monkey physical cognition abilities (but see e.g. Amici et al. 2010; Manrique

et al. 2010, 2011; Schmitt et al. 2012, 2013). While Manrique and colleagues (2010; 2011) compared the performance of apes and capuchins at selecting tools with appropriate compliant properties, to my knowledge there have been no direct comparisons of monkeys and apes in terms of their planning ability in a physical problem-solving context. This should be rectified, given that an ability to assess alternative possible action sequences and select between them has been posited as one way in which apes and monkeys may differ cognitively (Barrett 2003). It would therefore be interesting to test Old and New World monkeys with the paddle-box (pilot work with capuchins and Barbary macaques suggested that this would be feasible), to see if monkeys would solve the sequential planning task. It would also be interesting to see if spider monkeys, which have previously demonstrated impressive inhibitory control skills (e.g. Amici et al. 2008, 2010), might outperform apes in the advance planning paddle-box task. If so, this would provide a strong indication that inhibitory control may indeed pose peripheral demands in this task.

8.2.3 Modelling tasks and simulating behaviour

A relatively new approach in the field of animal cognition has been to use cognitive modelling (e.g. van der Vaart et al. 2011, 2012; Chappell and Hawes 2012) to produce simulations of behaviour, to help to distinguish between alternative explanations and provide insight into how animals might be solving problems. Chappell and Hawes (2012) generated 'problem descriptions' representing the 64 unique puzzle-tube configurations presented to orangutans by Tecwyn et al. (2012; chapter 2 of this thesis). The information that the 'virtual orangutan' possessed could be manipulated (e.g. it might have known about the tube end pieces but not gap width), and different models were run to generate simulations of behaviour. The outputs of the different models were then compared to the behaviour of the real orangutans on a trial-by-trial basis. If a particular model generates similar patterns of performance to a test subject (i.e. model and subject succeed in the same trials and fail in the same trials) then this may provide some insight into the knowledge possessed by that individual, and what cues they may have been using when attempting

to solve the task, therefore providing an excellent method for examining inter-individual variation (Chappell and Hawes 2012). Perhaps more importantly still, such models could be used to highlight any issues with a novel piece of apparatus or planned experimental design, thus permitting any creases to be ironed out *before* running experiments with real animals (Chappell and Hawes 2012).

8.3 Concluding remarks

Despite a wealth of animal cognition research in recent years, we still have little idea how animals solve novel problems in terms of the underlying mechanisms involved, and which cognitive processes are shared between species, including humans. This can only be probed with carefully focused experimentation. It is essential that continuing efforts are made to develop novel tasks suitable for testing the physical problem-solving skills of a broad range of species, particularly given the growing interest in the convergent evolution of cognition. Developing methodologies that could easily be adapted to test distantly related, anatomically diverse species (e.g. primates and birds) will be key to progress in the field of comparative physical cognition, as it is the only way in which valid inferences regarding the evolution of cognitive abilities can be drawn. Increased collaboration between labs and research groups to collect comparative data across a wide range of species using standardised protocols would enable more rapid progress to be made.

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APPENDICES

Appendix A: Supplementary material for chapter 2

Gap-size task

Materials and methods

Four subjects participated in this task; the same three as in the task reported in the manuscript, plus Radja, a 47-year-old wild-born female, who was accompanied by a dependent juvenile during testing. The apparatus were the same as those used in the task reported in the manuscript, but for this task there was only one gap at each side of the puzzle-tube (two in total) and only two different gap-sizes (small and large). The apparatus were presented to each subject in 32 trial-unique configurations, pseudorandomised into four blocks of eight trials. Blocks were presented to subjects in a random order and subjects received one testing session per day. The general testing procedure and data scoring were the same as reported for the task in the manuscript. Two-tailed binomial tests (α=0.05, n=32 for each) were used to assess whether subjects' choice of initial direction differed from what would be expected by chance and also whether they showed any directional preferences.

Results

Amos', Sandy's and Silvia's performances did not differ significantly from chance-level (50% correct) across the 32 trials (binomial test: 17 trials correct, p=0.86; 16 trials correct, p=1.00; and 16 trials correct, p=1.00, respectively). Radja only chose the correct initial direction in 6 out of the 32 trials, which differed significantly from chance-level (binomial test: p=0.001). Table A1 gives a summary of subjects' performance across testing sessions.

Table A1 Summary of performance across session

Session	Amos			Sandy			Silvia			Radja		
	No. correct	1st trial correct?	block	No. correct	1st trial correct?	block	No. correct	1st trial correct?	block	No. correct	1st trial correct?	block
1	**4**	Y	2	**2**	N	4	**4**	N	4	**2**	N	4
2	**5**	N	3	**4**	Y	3	**3**	Y	2	**0**	N	1
3	**5**	Y	4	**5**	Y	1	**5**	Y	1	**1**	N	2
4	**3**	Y	1	**5**	Y	2	**4**	N	3	**3**	Y	3

Appendix B: Supplementary material for chapter 3

B1 Details of calculations of probabilities of succeeding by chance in the sequential planning task

Based on the premise that the paddle on which the food was located at any given point was rotated in a random direction, the probability of retrieving the reward in each of the five different trial-types was as follows: 1 step, 1 solution: 0.5

2 steps, 2 solutions: (0.5 * 0.5) * 2 = 0.5

3 steps, 3 solutions (see Fig. B1): (0.5 * 0.5 * 0.5) * 3 = 0.375

2 steps, 1 solution: (0.5 * 0.5) = 0.25

3 steps, 1 solution: (0.5 * 0.5 * 0.5) = 0.125

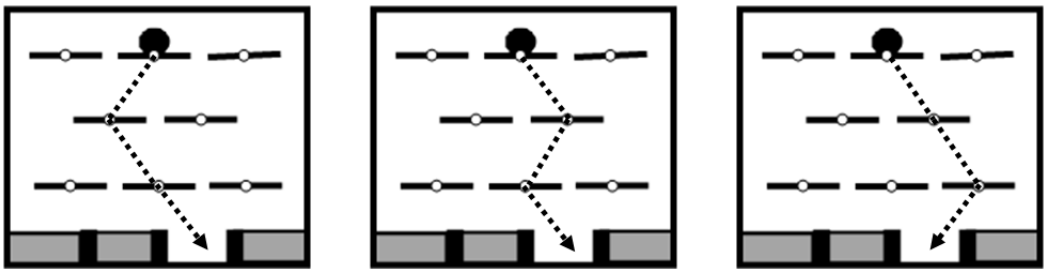

Fig. B1 Schematic diagram of the paddle-box apparatus showing the three different ways in which the reward could be retrieved in a 3 steps, 3 solutions trial

B2 Binomial test results for each subject in each trial type in the sequential planning task

Table B2 Performance of each subject in each of the different trial types in experiment 2. Bold *P* values indicate significance in a binomial test (alpha=0.05)

Species	Subject	1 step, 1 solution		2 steps, 2 solutions		3 steps, 3 solutions		2 steps, 1 solution		3 steps, 1 solution	
		binomial proportion = 0.5		binomial proportion = 0.5		binomial proportion = 0.375		binomial proportion = 0.25		binomial proportion = 0.125	
		Trials correct	***P***	**Trials correct**	***P***	**Trials correct**	***P***	**Trials correct**	***P***	**Trials correct**	***P***
Bonobo	Cheka	15/18	**0.008**	4/4	n/a	10/10	**<0.001**	12/14	**<0.001**	5/9	**0.002**
Bonobo	Keke	19/20	**<0.001**	4/4	n/a	10/10	**<0.001**	10/16	**0.002**	7/10	**<0.001**
Bonobo	Kichele	8/14	0.791	1/3	n/a	5/8	0.137	5/8	0.321	1/4	n/a
Orangutan	Amos	13/16	**0.021**	2/4	n/a	4/8	0.349	5/12	0.158	4/8	0.067
Orangutan	Sandy	16/16	**<0.001**	4/4	n/a	8/8	**<0.001**	12/12	**<0.001**	7/8	**<0.001**
Orangutan	Jingga	12/16	0.077	4/4	n/a	6/8	0.036	11/12	**<0.001**	7/8	**<0.001**
Orangutan	Yuno	16/16	**<0.001**	4/4	n/a	7/8	**0.006**	6/12	0.054	5/8	**0.001**
Orangutan	Jewel	15/16	**<0.001**	3/4	n/a	5/8	0.137	8/12	**0.03**	6/8	**<0.001**
Orangutan	Tjintah	14/16	**0.004**	2/4	n/a	5/8	0.137	10/12	**<0.001**	7/8	**<0.001**
Orangutan	Anak	15/16	**<0.001**	1/4	n/a	6/8	**0.036**	7/12	**0.014**	4/8	**0.011**

B3 Results of sequential planning with goal change between trials experiment

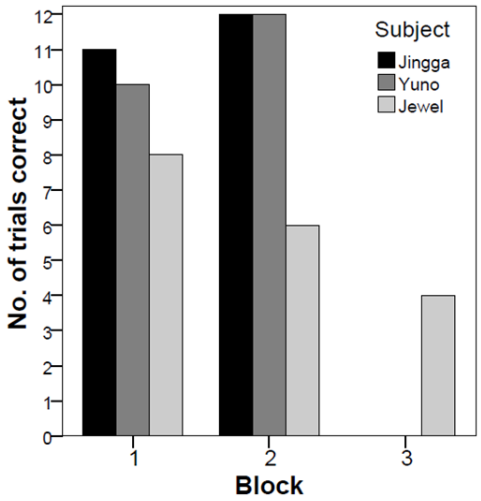

Fig. B3 Number of correct trials (out of 12) for each subject across consecutive testing blocks when the goal location was switched between trials. Only Jewel received the third block of trials because Jingga and Yuno performed perfectly in block 2

Appendix C: Supplementary material for chapter 7

Table C1 Standardised descriptions of primate positional behaviour. Locomotor and postural modes are taken from Hunt (1996) and Thorpe and Crompton (2006). Dynamic postures describe additional behaviours defined for this study

POSITIONAL BEHAVIOUR	DEFINITION
LOCOMOTION: compressive	
Quadrupedal walk	Locomotion on top of supports angled at <45°; typically all the four limbs contact the support in a particular sequence. The torso is pronograde or roughly parallel to the support.
Tripedal walk	Same as quadrupedal walking in its various expressions, except one limb is not used in locomotion, the other often being used to grasp a carried object.
Bipedal walk	The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. Hip and knee may be extended or flexed.
LOCOMOTION: suspensory	
Orthograde forelimb suspensory	Classic hand over hand orthograde suspensory locomotion in which the forelimbs bear more than half of the body weight, but in which some support from the hindlimbs may occur. The humerus is completely abducted and the elbow is extended.
Hindlimb swing	Body is held upside-down, and animal swings on one or both hindlimbs. Often used as intermediary form of locomotion to reorient body between two longer bouts of different locomotor modes.
Forelimb-hindlimb swing	Suspensory locomotion which may or may not follow regular limb sequence, utilizing both forelimbs and hindlimbs in both orthograde and pronograde positions.
Pronograde suspensory	Three or four hands/feet are used in some combination; the torso is pronograde, and limbs are in tension. Regular gaits are common.
POSTURE: compressive	
Lie	Torso pronograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso.
Sit/squat	The ischia bear substantial portion (usually more than half) of the body weight; the torso is relatively orthograde/the body weight is borne solely by the feet/foot, both hip and knee are strongly flexed.
Orthograde stand	Standing on the hindlimbs with no significant support from any other body part. The torso is near-orthograde. The hip and knees are may be extended or flexed.
Pronograde stand	Four- or three-limbed standing on horizontal or subhorizontal supports, the elbow and knee are (relatively) extended and the trunk is near horizontal.
POSTURE: suspensory	
Orthograde forelimb suspend	Posture wherein more than half of the body weight is borne by the forelimb(s) grasping a support above the animal's centre of mass.
Hindlimb suspend	Suspension from one or both hindlimbs, with both hips and knees extended.
Orthograde quadrumanous suspend	Orthograde suspend where body mass may be supported by one or both hindlimbs in equal or greater proportion than one or both forelimbs.
Forelimb-hindlimb suspend	Suspension by a forelimb and a foot with the trunk in a subhorizontal orientation. Limbs are typically extended.
Pronograde suspend	Inverted pronograde suspension involving both hindlimbs and one or both forelimbs.

DYNAMIC POSTURE: compressive	
Sit/squat+bounce	As for sit/squat, but downward force using the body mass is repeatedly applied at a single point along a horizontal support causing the support to deflect downwards. Forelimb(s) are usually in contact with additional supports.
Tripedal stand+bounce	As for tripedal stand, but downward force using the body mass is repeatedly applied at a single point along a horizontal support causing the support to deflect downwards.
DYNAMIC POSTURE: suspensory	
Orthograde forelimb suspend+bounce	As for forelimb suspend, but downward force using the body mass is repeatedly applied at a single point along a horizontal support causing the support to deflect downwards.
Hindlimb suspend+bounce	As for hindlimb suspend, but downward force using the body mass is repeatedly applied at a single point along a horizontal support causing the support to deflect downwards.
Pronograde suspend+bounce	As for pronograde suspend, but downward force using the body mass is repeatedly applied at a single point along a horizontal support causing the support to deflect downwards.
Orthograde forelimb suspend+swing	As for forelimb suspend, but the subject repeatedly swings its body mass back and forth around a single pivot point on a horizontal support. Swinging may be parallel or perpendicular to the support.
Hindlimb suspend+swing	As for hindlimb suspend, but the subject repeatedly swings its body mass back and forth around a single pivot point on a horizontal support. Swinging may be parallel or perpendicular to the support.
Pronograde suspend+swing	As for pronograde suspend, but the subject repeatedly swings its body mass back and forth around a single pivot point on a horizontal support. Swinging may be parallel or perpendicular to the support.